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The Oxygen Requirement of Plant Roots in Relation to Soil Aeration.

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INTRODUCTION.

The general opinion that a high degree of soil aeration is necessary to the proper respiration of plant roots and hence to favorable growth proves, on examination, to have a very inadequate basis of observed fact. Actual experiments on the respiration of roots are meagre and inconclusive. Experiments and observations on the practical benefits of improved soil aeration are more numerous but nearly all of them have lacked adequate controls or have failed to take into account the many chemical, bacterial and other secondary reactions which are known to complicate the problem. The assumption of the dependence of root respiration upon adequate soil aeration appears to have arisen largely from various items of indirect and inferential evidence which may be summarized under three heads: The known necessity of oxygen for the respiration and life of protoplasm in general; The possession by plants of internal aerating systems and other morphological devices which appear to be useful in supplying oxygen to organs not directly exposed to the air; The observed beneficial effects of good aeration in cultural practice. The implication of these evidences is strong but certain contrary indications are also known. For instance, some organisms and parts of organisms do not require free oxygen for respiration. Again many plants do not

possess special aerating systems and it is by no means certain that these systems, even when present, are adequate for the transfer of respiratory oxygen to the remoter organs such as the roots. The cultural benefits of soil aeration may be ascribed, with much probability, to secondary chemical and bacteriological changes in the soil rather than to direct effects on root respiration. Nor is there lacking direct evidence against the assumption of the necessity for free oxygen in the soil. For instance, roots of some plants are known to penetrate many feet into the soil. Other roots live habitually, or may live for a time, in the water-saturated soils of marshes and stream banks. It is difficult to see how such deep-lying or hydrophyllous roots can obtain any considerable supply of atmospheric oxygen even when all possible allowance is made for supply by means of internal aerating systems.

Because of these uncertainties and conflicting implications it seemed desirable that the whole matter be reviewed, both with regard to information available in the literature and from practice, and by actual experiment. The results of this review are embodied in the present paper. I am indebted to Professor B. E. Livingston for the suggestion of the problem and for much detailed and invaluable advice, assistance and inspiration in the planning of the experimental work. I am also indebted to Dr. W. A. Cannon of the Department

of Botanical Research of the Carnegie Institution of Washington for placing his unpublished material at my disposal and for continuous advice and suggestion. Dr Cannon's experiments will be reviewed in detail below. In the actual conduct of the experiments I have been assisted from time to time by Mr. Herbert F. McCall, Mr. Sam F. Trelease, Mr. F. M. Hildebrandt, Mr. Frederick Witte and Mr. William A. Schaefer. Mrs. Grace J. Livingston has assisted importantly in the preparation of the bibliography and the verification of references.

The investigation of this problem might take either one of two directions; the study of the composition of soil air, or the direct investigation of the oxygen requirements of plant roots. In the experimental part of the present investigation it is the second line that has been followed. The precise study of the composition of the soil air is a matter of extreme difficulty, and assurance in the correctness of results would be almost impossible to obtain without an impossibly large amount of observation and experiment. In drawing air samples from the soil there is always a chance of downward leakage from the atmosphere, of abnormal soil permeability, of bacterial or chemical abnormality, or of some other exceptional circumstance. On the other hand experiments on the oxygen requirement of roots are comparatively simple and are susceptible of precise control. Although the experimental work here reported is entirely

in this latter field, a preliminary chapter is devoted to the existing data concerning the composition of the soil air and to the possibilities and probabilities in this connection.

The contradictions of evidence outlined in the opening paragraph of this introduction imply that an explanation may lie in the variability of different species of plants with regard to oxygen needed by their roots; some species requiring an ample supply, some species being able to exist with little or none. It will appear below that this suggestion receives conclusive support ~~for~~ from the results of the experimental work.

INFERENTIAL EVIDENCE OF THE NEED OF ROOTS FOR OXYGEN.

It was mentioned in the introduction that the customary assumption of the need for soil aeration rests on inferential evidence of three kinds:, physiological (the necessity of oxygen for protoplasmic respiration), morphological (the aerating systems of plants), and cultural (the agricultural benefit and ecological significance of good soil aeration). This inferential evidence must be examined a little more in detail; as also the existing facts which have contrary implications.

The general existence of, and need for, protoplasmic respiration of the usual character is too well known to require review.[1] Nearly all experiments, however, have been made on entire plants or on their aerial portions or else on free-living plants such as algae or bacteria. Experiments on ~~root~~ respiration in underground organs have been confined largely to work with beets, potatoes and similar

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[1] See the summaries of Palladin,- Pflanzenphysiologie, pp. 179-211 (1911) and Bayliss,- Principles of General Physiology, pp. 580-636 (1915), also Vernon- Biochemistry of Respiration,- Science Prog. 9: 251-269 (1914).

massive structures ~~tubers~~,[1] mostly separated from the ~~parent~~ rest of the plant. However, determinations of the respiration of normal, living roots have been made by several investigators[2] and the well known fact of the frequent excretion of carbon

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[1] Heintz,- Bot. Jahresber. 1873: 358; Müller-Thurgau,- Landw. Jahrb. 14: 851 (1885); Kny,- Ber. deut. bot. Ges. ______: 164 (1889); Devaux,- Bull. Soc. bot. 37: 257 (1890); Böhm,- Verh. Zool.-Bot. Ges. Wien 42: 47 (1892); Ziegenbein,- Jahrb. wiss. Bot. 25: 563 (1893); Richards,- Ann. Bot. 10: 531 (1896), 11: 29 (1897); Wilms,- Jour. Landw. 47: 261 (1899); Vöchting,- Bot. Ztg. 1: 91 (1902); Stocklasa,- Beitr. Chem. Physiol. u. Path. 3: 473 (1903); Strohmer,- Oest. Zeits. Zuckerind. 31: 933 (1903), 32: 1 (1903); Ehrenberg,- Zeits. für Pflanzenkrankh. 16: 193 (1905); Duggar and Hill,- Science 33: 201 (1911); Appleman,- Maryland Agr. Exp. Sta., Bull. 183 (1914), Bull. 191 (1915); Hasselbring and Hawkins,- Jour. Agr. Res. 5: 509-517 (1915).

[2] de Saussure,- Recherches chimiques, pp. 8, 60-61 (1904); Nobbe,- Landw. Vers. Stat. 7: 451 (1865); Deherain and Vesque,- Ann. Sci. nat. (6) 3: 327 (1876); Saikewicz,- Bot. Jahresber. 1877: 722, Ann. Agron. 7: 476 (1882); Cauvet,- Bull. Soc. Bot. 27: 113 (1880); Palladin,- Ber. deut. bot. Ges. 4: 322 (1886); Areboe,- Forsch. Geb. Agr. Phys. 16: 450 (1893).

dioxide by roots[1] is another evidence that in many cases at least, roots actually do respire much as do the aerial portions of plants.[2] This does not mean, however, that all roots respire in the normal manner or that respiration by means of free oxygen is the only kind of respira-

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1. Knop,- Ann. Chem. Pharm. 129: 287 (1864); Corenwinder,- Ann. sci. nat. (5) 9: 63 (1868); Deherain and Vesque,- C. R. 84: 959 (1877); Czapek,- Jarhb. wiss. Bot. 29: 321 (1896); Hall,- Science Prog. 1: 51-57 (1906); Stoklasa and Ernest,- Centbl. Bakt., Abt. 2, 14: 723-736 (1905), Zeits, Zuckerind. Böhmen 31: 291-307 (1907), Jahrb. wiss. Bot. 46: 55-102 (1908); Reed,- Pop. Sci. Mon. 73: 257-266 (1908). Quantitative experiments on the amount of CO_2 excreted by roots have been made by Kossowitsch but apply to water-cultures only. Zhur. Opyt. Agron. 5: 482-493 (1904), 7: 251 (1906).

2. The supposed aerotropism of roots reported by Molisch has been questioned by Bennett and Sammet and is probably hydrotropism: Molisch,- Situngsber. Akad. Wiss., Wien, Abt. I, 90: 194 (1884), 102: 423 (1893); Bennett,- Bot. Gaz. 37: 241 (1904); Sammet,- Jahrb. wiss. Bot. 41: 611 (1905). Upward curvature of roots in water-logged soils has been observed by several authors; see Jost,- Bot. Ztg. 45: 169 (1887); Goebel,- Bot. Ztg. 45: 717 (1887); Schenk,- Jahrb. wiss. Bot. 20: 534,564, 569 (1889); Wieler,- Jahrb. wiss. Bot. 32: 503 (1898). It is possible, however, that this may be due to negative

hydrotropism or, more likely, to a disturbed geotropism resulting from lack of oxygen, rather than to an actual positive aerotropism. See Ewart,- Trans. Liverpool Biol. Soc. 8: 240 (1894); 10: 191 (1896) and Pfeffer,- Physiology of Plants, vol. 3, p. 182 (1906).

tion of which roots are capable. The existence of anaerobic bacteria is common knowledge[1] and it is even more significant for the present problem that many organisms are able to live either aerobically or anaerobically, suiting their metobolism to the

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[1] The classical investigations are those of Pastuer on the butyric bacteria, C. R. 52: 344-347 (1861). For summaries of more recent work see Chudiakow,- Kochs Jahresber. 1897: 44, Centbl. Bakt., Abt. II, 4: 389 (1898); Porodko,- Jahrb. wiss. Bot. 41: (1904); Lesser,- Ergeb. Physiol. 8: 742-796 (1909); Marshall,- Microbiology, 2nd ed. pp. (1916). On anaerobic worms see Bunge,- Zeits. physiol. Chem. 8: 48 (1883), 12: 565 (1888); Weinland,- Zeits. Biol. 42: 55-90 (1901), 43: 86-111 (1902), 45: 113-116 (1904), 45: 517-531 (1904), 48: 87-143 (1906). On anaerobic protozoa see Pütter,- Zeits. allg. Physiol. 5: 566 (1905).

nature of their surroundings.[1] If long continued existence and successful reproduction form the criteria, this anaerobic existence appears to be confined to lower organisms. However, it is now well known that temporarily anaerobic existence is possible to many of

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[1] On facultative anaerobic bacteria see the authors cited in the last note also: Kitt,- Centbl. Bakt. 17: 168 (1895); Kedrowski,- Zeits. Hyg. 20: (1895); Chudiakow,- Centbl. Bakt. 4: 392 (1895); Ritter,- Flora 85: 135 (1898), 86: 329 (1899). On Mucor see: Pasteur,- Etudes sur la biere, pp. 130-132 (1876); Kostytschew,- Centbl. Bakt., Abt. II, 13: 490 (1904); Wehmer,- Centbl. Bakt., Abt. II, 14: 556 (1905), 15: 8 (1905). On the alcohol yeast see Pasteur,- Etudes sur la biere (1876); Beijerinck,- Arch. neelandaises 29: 1 (1894); Iwanowski,- Zap. Akad. Nauk, St. Petersburg 73: heft 2 (1894); Korff,- Centbl. Bakt., Abt. 2, 4: 465-472 (1898), 12: 501-507 (1899), 13: 529-535 (1899), 14: 561-569 (1899), 15-16: 616-627 (1899); Brown,- Ann. Bot. 28: 197-226 (1914).

the higher plants[1] and that many vital functions can go on for days or weeks in the entire absence

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[1] The earlier literature is open to question because of the possible presence of micro-organisms. For reviews see Pfeffer,- Physiology of Plants, vol. 1, pp. 538-539 (1900) and Hill,- Cornell Agr. Exp. Sta., Bull. 330, pp. 379-387 (1913). Of the very voluminous recent literature see especially; Detmer,- Ber. deut. bot. Ges., 10: 201-205 (1892); Palladin,- Rev. gen. bot. 6: 201 (1894), Pflanzenphysiologie, pp. 201-202 (1911); Palladin and Kostytschew,- Zeits. physiol. Chem. 48: 214-239 (1906); Kostytschew,- Ber. deut. bot. Ges. 20: 327 (1902), 24: 436 (1906), 25: 178 (1907), 26a: 167 (1908), Scripta Bontanica 25: (1907); Godlewski and Polzenius,- Bull. Acad. sci. Cracovie ____: 267 (1897), __: 227 (1901); Nabokikh,- Zhur. Opyt. Agron. 4: 696-713 (1903), Ber. deut. bot. Ges. 21: 467-476 (1903), Landw. Jahrb. 38: 51-194 (1909); Lesser,- Ergeb. Physiol. 8: 742-796 (1909); Lehman,- Jahrb. wiss. Bot. 49: 61-90 (1911). Kostytschew (Scripta Bot., loc. cit.) and Nabokikh (Landw. Jahrb., loc. cit.) give bibliographies of further literature.

of atmospheric oxygen.[1] Indeed the theories of respiration now current regard free oxygen as unnecessary for the essentials of the process. The important reactions are believed to be enzymatic splittings of carbohydrates and the like, and oxygen is regarded as necessary only for the

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[1] On anaerobic excretion of carbon dioxide and other respiratory products see Palladin, Kostytschew and Nabokikh; *loci citati* in last note. On protoplasmic streaming in the absence of oxygen see Lopriore,- Jahrb. wiss. Bot. *28*: 576 (1895); Ewart,- Jour. Linn. Soc. Bot. *31*: 420 (1896), *33*: 123 (1897); Farmer,- Ann. Bot. *10*: 288 (1896); Kühne,- Zeits. Biol. *35*: 43 (1897), *36*: 1 (1898); Ritter,- Zeits. Biol. *36*: 351 (1898); Celakowski,- Bull. Acad. Sci. de Bohme ____: (1898). On movements of Drosera and Mimosa in absence of oxygen see Correns,- Flora *75*: 87, 144 (1892). On other movements see Celakowski *loc. cit.* In general growth will not occur in the absence of oxygen but slight anaerobic growth has been observed in seedlings of *Helianthus annuus*: Wieler,- Unters. bot. Inst. Tübingen *1*: 200, 223 (1883); Nabokikh,- Bot. Centbl., Beih. *13*: 272 (1902). Nabokikh (*loc. cit.*) and Czapek,- Jahrb. wiss. Bot. *27*: 277 (1895),

In general growth will not occur in the absence of oxygen but slight anaerobic growth has been observed in seedlings of Helianthus annus: Wieler,- Unters. bot. Inst. Tübingen 1: 200, 223 (1883); Nabokikh,- Bot. Centbl., Beih. 13: 272 (1902). Nabokikh (loc. cit.) and Czapek,- Jahrb. wiss. Bot. 27: 277 (1895), have observed the continuance of the geotropic response in the absence of oxygen. The continuance of the division of the nucleus in the absence of oxygen is reported by Demoor,- Arch. Biol. 13: 76 (1894). Germination of rice seeds in the absence of oxygen has been reported by Takahashi (Bull. Coll. Agr., Tokyo Imp. Univ. 6: 439-442 (1905)) and confirmed by Demoussy (C. R. 145: 1194-1196 (1907)), Akemine (Landw. Ztg. 63: 78-93 (1914)) and Free (unpublished experiments).

oxidation and removal of intermediate products which would be toxic if allowed to accumulate.[1] In anaerobic respiration these products do accumulate as witness the production of alcohol during the (temporary) anaerobic

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[1] The first suggestion toward this theory was by Pfeffer,- Abh. Kgl. Sächs Ges. Wiss., Math.-phys. kl. 15: 449 (1889). Later development has been largely by Palladin and by Bach. See especially: Palladin,- Ber. deut. bot. Ges. 23: 240-247 (1905), 26: 378, 389 (1908) 27: 444 (1910), Biochem. Zeits. 18: 151-206 (1909), 27: 441 (1910), 35: 1-18 (1912), Izv. Akad. Nauk (St. Petersburg) ____: 937 (1912), Zeits. für Gärungsphysiol. 1: 91 (1912), Fiziologia Rastenakh (Plant Physiologie) 7th Russian ed. pp. 210, 216, 224-225, 241-245 (1914) (Note,- The German edition of this work is from the sixth Russian edition and does not contain the new developments of the respiration theories. The forthcoming English edition edited by B. E. Livingston will be corrected to the eighth Russian edition and will contain the material here cited); Palladin and Sabinin,- Biochem. Jour. 10: 183-196 (1916); Bach,- C. R. 124: 951-954 (1897), Biochem. Zeits. 31: 443-449 (1911), Arch. sci. phys. et nat. 32: 27-41 (1911), Oppenheimer's Handbuch der Biochemie, Ergänzungsb., pp. 133-182 (1913), Biochem. Zeits. 52: 412-417 (1913); Bach and Battelli,- C. R. ___: (June 2, 1903), Chodat and Bach,- Arch. sci. phys. et nat. 17: 477 (1904). For a recent review see Appleman,- Maryland Agr. Exp. Sta., Bull. 191, 16 pp. (1915).

respiration of higher plants, germinating seeds, etc.[1] When the accumulation is sufficient to poison the organism, respiration stops and death ensues. From this viewpoint anaerobes are merely organisms which are able to withstand the intermediate products of the respiration process, or what comes to the same thing, which can so modify their metabolism as to produce intermediate products which are harmless. The facultative anaerobes make this adjustment easily and are able to live either under conditions of oxidation of their intermediate products by atmospheric oxygen or in situations where oxygen is absent, where such oxidation is impossible and where, therefore, the intermediate products accumulate. If the intermediate products could be removed or otherwise disposed of, all organisms would be facultative anaerobes. That some steps in this direction are possible is indicated by the fact that the food supply and other surrounding conditions alter

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[1] See references on anaerobic respiration on page 11, note 1, also: Brefeld,- Landw. Jahrb. 5: 327 (1876); Maze,- C. R. 128:1608 (1899), Ann. Inst. Pasteur 14: 350-368 (1900); Godlewski and Polzeniusz,- Ann. Agron. 28: 151-165 (1902); Matruchot and Molliard,- Rev. gen. bot. 15: 193 (1903); Nabokikh,- Zhur. Opyt. Agron. 5: 305-315 (1904); Stoklasa,- Zeits. physiol. Chem. 48: 214 (1906); Palladin and Kostytschew,- Ber. deut. bot. Ges. ____: 51 (1907); Ivanov,- Ber. deut. bot. Ges. 29: 622-629 (1912).

the amount of oxygen required for respiration and the length of time that anaerobic conditions can be endured, both by lower organisms and by the higher plants.[1] Specific experimental attack on this problem might lead to much greater extensions of facultative anaerobiosis. It seems not improbable that differences in the capacity to dispose of intermediate respiration products may explain the very different respiration rates of differ-

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[1] On higher plants see authors cited on page 11, note 1, especially Palladin and Nabokikh, also: Godlewski,- Bull. Acad. sci. Cracovie ____: (1904); Lehman,- Biochem. Zeits. 50: 388 (1913). On the effects of food materials on anaerobiosis of bacteria see: Liborius,- Zeits. für Hyg. 1: 172 (1886); Kitasato and Weyl,- Zeits. für Hyg. 8: 49, 9: 17 (1890); Winogradsky,- C. R. 116: 1385 (1893), 118: 353 (1894), Arch. sci. biol. Inst. med. exp. St. Petersb. 2: 297 (1895); Kedrowsky,- Zeits. für. Hyg. 20: (1895); Kitt,- Centbl. Bakt., 17: 168 (1895); Marshall,- Microbiology, 2nd ed. pp. (1916).

ent tissues and plant species,[1] though the prevailing rates of growth and of other metobolic processes ~~will~~ should

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[1] On variations of respiration rate in different species see: Bert,- C. R. 86: 443, 1276 (1873), "La pression barometrique" (1878); Godlewski,- Jahrb. wiss. Bot. 13: 522 (1882); Wieler,- Unters. bot. Inst. Tübingen 1: 189 (1883); Bonnier and Mangin,- Ann. sci. nat. (6) 17: 265, 18: 359, 19: 246 (1884); Mangin,- C. R. 122: 747 (1896); Stich,- Flora ____: 1(1891); Aubert,- Rev. gen. Bot. 4: 203 (1892). On variations between different plant organs (e.g. flowers, tubers, etc.) see the authors cited above in this note, also on page 7 , notes 1 and 2. ~~page , note~~ , also Garreau,- Ann. sci. nat. (3) 15: 1 (1851), and Nabokikh,- Bot. Centbl. Abt. 1, Beih. 26: 7-149 (1910). Earlier literature is cited by Pfeffer,- Physiology of Plants, vol. 1, pp. 524-526. On variations among mosses, fungi and algae see: Bonnier and Mangin,- *loc. cit. supra*; Diakonow,- Ber. bot. Ges. ____: 3 (1886); Jumelle,- Rev. gen. Bot. 4: 112 (1892); Jönsson,- C. R. 109: 440 (1894); Münch,- Naturw. Zeits. Forst- und Landw. 7: 57-75, 87-114, 129-160 (1909); Maige,- Bull. Soc. Hist. Nat. Afrique Nord ____: 29-31 (1909); Chambers,- Ann. Rep. Missouri Bot. Gard. 23: 171-207 (1912). On variations among bacteria see authors cited on page 9 , note 1 , page 10 , note 1 , and page 15 , note 1 , also Hesse,- Zeits.

für Hyg. 15: 183 (1893). On variations in amount of oxygen required for different plant movements see Correns,- Flora 75: 87, 97, 146 (1892). On variations in oxygen requirement of various germinating seeds see Takahashi, Demoussy and Akemine, loci citati on page , also Bert,- C. R. 76: 1493, 77: 531 (1873), 80: 1579 (1875); Rischawi,- Landw. Vers. Stat. 19: 321 (1876); Mazé,- Ann. Inst. Pasteur, 14: 350-368 (1900); Schaibbe,-Beitr. wiss. Bot. von Fünfstick 4: 93 (1900); Nabokikh,- Ber. deut. bot. Ges. 19: 222 (1901); Godlewski and Polzeniusz,- Ann. Agron. 28: 151-165 (1902); Dude,- Flora 92: 205 (1903); Crocker,- Bot. Gaz. 44: 375-380 (1907), Am. Jour. Bot. 3: 112 (1916); Becker,- Inaug. Diss., Münster, 1911; Gassner,- Jahrb. Ham. wiss. Anstalt., Beih. 1, p. 29 (1911); Shull,- Bot. Gaz. 52: 453-477 (1911), 57: 64-69 (1914); Atwood,- Bot. Gaz. 57: 386 (1914). On the exceptionally low respiration of certain water and swamp plants see: Garreau,- loc. cit. supra, also: de Saussure,- Recherches chimiques sur sur la vegetation, Paris, 1804 (Ostwald's Klassiker, Nos. 15 and 16); Freyberg,- Landw. Vers. Stat. ____: 463 (1879); Devaux,- Ann. sci. nat. (7), 9: 35-40 (1889).

be important also. Of the many possible intermediate products ethyl alcohol is perhaps the most common,[1] but it is probable that organic acids are very common also, especially in the normal respiration which is completed at once by the action of atmospheric oxygen.[2]

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[1] See page 14 , note 1 .

[2] On production of organic acids in plants see Mayer,- Die Sauerstoffabscheidung fleischiger Pflanzen, 1876; Krause,- Die Stoffwechsel bei den Crassulaceen, Abh. Nat. Ges. Halle, 16, 1886, Flora ____: 54 (1897); Warburg,- Unters. bot. Inst. Tübingen 2: 53 (1886). Other literatute is cited by Pfeffer,- Physiology of Plants, vol. 1, pp. 327-329, 485-491 (1900) and Haas and Hill,- Chem. of Plant Products, pp. ( ). On the production of lactic acid in muscle see Bayliss,- Principles of General Physiology, pp. 441-451 (1915). Propionic acid is produced by certain anaerobic worms, Weinland,- Zeits. Biol. 42: 55-90 (1901). On the recent work of MacDougal, Richards, Spoehr and associates on the relations between respiration, acid formation and growth in cacti see: MacDougal,- Physiol. Res. 1: 289-292, 292-298 (1915), Car. Inst. of Wash. Yearbook 14: 57-59, 71-72 (1915), 15: 61-62 (1916), Bull. N. Y. Bot. Gard. ____: (1916); Richards,- Car. Inst. of Wash., Yearbook 10: 66 (1911), 11: 65-66 (1912), 12: 84-86 (1913), 13: 89-91 (1914), Car. Inst. of Wash.,

Pub. No. 209, 107 pp., 1915; Spoehr,- Car. Inst. of Wash., Yearbook 10: 65-66 (1911), 11: 63-65 (1912), 12: 82-83 (1913), 14: 64-65 (1915), 15: 54-55 (1916), Biochem. Zeits. 57: 95-111 (1913), Bot. Gaz. 59: 366-386 (1915); Spoehr and Estill,- Car. Inst. of Wash., Yearbook 14: 66 (1915); Long,- Car. Inst. of Wash., Yearbook, 13: 91-92 (1914), 14: 69-71 (1915), Plant World 18: 261-272 (1915), Bot. Gaz. 59: 491-497 (1915), Physiol. Res. 1: 298-315 (1915); Edith B. Shreve,- Plant World 18: 297-343 (1915), Car. Inst. of Wash., Yearbook, 15: 64-66 (1916), Physiol. Res. 2: 73-127 (1916). On the production of acids by bacteria and other lower organisms see authors cited on page 9, note 1, page 10, note 1 and page 15, note 1, also literature cited by Pfeffer,- Physiology of Plants, vol. 1, pp. 485-489, 527-528 (1900), and Marshall,- Microbiology, 2nd ed. pp. (1916).

Many other compounds appear to occur occasionally, since they are formed by certain organisms, especially bacteria, and more especially under anaerobic conditions.[1]

On this conception of respiration the customary occurrence of aerobic respiration in a given organism is no evidence that anaerobic respiration is impossible to it. The fact that certain roots do, under ordinary conditions, respire aerobically does not prove that these same roots might not respire anaerobically under other conditions. Still less is it possible to extend to roots in general, conclusions drawn from the respiratory behavior of the roots of a single species or of a few species. The essential matter would be the possibility of avoiding the production of, or procuring the adequate disposal of, intermediate respiration products which are toxic. The abilities of roots in this connection are probably widely varied. It is known that when the oxygen supply is low, as in swamp soils, the customary excretion of carbon dioxide by roots is replaced in part by the excretion of other substances many of which are toxic

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[1] The compounds include methane, carbon monoxide, hydrogen sulphide, amyl, butyl and other alcohols, leucine, tyrosine and many amines, indol, skatol, several mercaptans, etc. For details see Löhnis,- Landwirtschaftliche Bakteriologie, 1910; and Kossowicz,- Bodenbakteriologie, 1912. On the bacteria which reduce compounds of sulphur, nitrogen and iron see, e.g., Kossowicz,- loc. cit. pp. 16-74 (1912).

and the presence of which is responsible for the production of an "acid" or "sour" soil which is consequently infertile.[1] These toxins are probably the intermediate products of the partial respiration which

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[1] On acid excretions by roots in the presence of insufficient oxygen see especially: Stoklasa and Ernest,- Jahrb. wiss. Bot. 46: 55-102 (1908), also: Stiehr,- Inaug. Diss., Kiel, 1903; Schreiner and Reed,- Bull. Torrey Bot. Club. 34: 279-303 (1907); Schleichert,- Naturw. Wochenschr. 22: 91-94 (1907); Reed,- Pop. Sci. Mon. 73: 257-266 (1908). On dihydroxystearic acid, a particular toxin found in badly aerated soils see: Schreiner and Shorey,- U. S. Bureau of Soils, Bull. 53, 53 pp., 1909; Schreiner and Skinner,- U. S. Bureau of Soils, Bull. 70, 98 pp., 1910; Schreiner and Lathrop,- Jour. Amer. Chem. Soc. 33: 1412-1417 (1911). On "sour" soils in general see Cameron,- The Soil Solution, pp. (1912), and Russel,- Soil Conditions and Plant Growth, 2nd ed., pp. 113-116 (1915) and literature cited by these authors. On the toxins of bog waters and soils see: Livingston,- Bot. Gaz. 37: 383-385 (1904), 39: 348-355 (1905); Dachnowski,- Bot. Gaz. 46: 130-143 (1908), 47: 389-405 (1909), 54: 503-514 (1912), Bull. Torrey Bot. Club 39: 53-62 (1912); Jodidi,- Mich. Agr. Exp. Sta., Tech. Bull. 4, 1909; Bauman and Gully,- Mitth. K. Bayr. Moorkulturanst. 4: 31-56 (1910; Bottomley,- Ann. Bot. 28: 531-540 (1914). Other literature is reviewed by Rigg,- Plant World, 19: 310-325 (1916).

alone is possible under such conditions. Some plants, common in swamps, have acquired partial immunity to these toxins.[1] Perhaps other plants are able to live under such conditions without producing toxins at all. Others may be able to dispose of toxins, as, for instance, by allowing them to pass upward with the transpiration stream to the aerial portions of the plant, where atmospheric oxygen is available to complete the ozidation. If respiration ~~be~~ were not too vigorous the transpiration stream might easily be competent to sweep out in this way all of the intermediate respiration products produced in the roots.. Once these products are removed to the aerial portions of the plant the completion of their oxidation presents no difficulty.

It is perhaps even more significant, especially for ecology and agriculture, that reactions occurring in the soil itself have much effect on the accumulation of these toxic intermediate products. All soils appear to have a certain power of destroying or removing these substances by oxidation, adsorption or in some other way now

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[1] Coville,- The agricultural utilization of acid lands by means of acid-tolerant crops, U. S. Dept. of Agr., Bull. 6, 1913.

unknown.[1] But certain soils possess this power in much higher degree than others. It is possible, therefore, that the ability of a root to live under conditions of deficient aeration may depend not only on the nature of the root and its own capacity for disposing of its intermediate respiration products, but also on the soil, through the degree to which it may possess the power of removing or rendering harmless the toxins excreted by the root. The available experimental data do not permit the discussion of these possible mutual effects of soil and plant on anaerobiosis of roots except in the most tentative and speculative way, but it is obvious that many varied behaviors are theoretically possible.

It is apparent, at the least, that the facts of respiration do not furnish a sound basis for assuming that all roots must be supplied with atmospheric

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1. True and Oglevee,- Bot. Gaz. 39: 1-21 (1905); König,- Landw. Vers. Stat. 66: 401-461 (1907); Schreiner and Reed,- Jour. Biol. Chem. 3: xxiv-xxv (1907), Jour. Amer. Chem. Soc. 30: 85-97 (1908), Bot. Gaz. 47: 355-388 (1909), U. S. Bur. of Soils, Bull. 56, 52 pp., 1909; Schreiner and Sullivan,- U. S. Bur. of Soils, Bull. 73, 57 pp., 1910, Bot. Gaz. 51: 121-130 (1911); Sullivan,- Jour. Biol. Chem. 6: xliv (1909); Sullivan and Reid,- Jour. Ind. and Eng. Chem. 3: 25-30 (1911).

oxygen or that good soil aeration is the uniformly necessary factor it is commonly supposed to be. The experimental part of this paper will show that the theoretical possibility of anaerobic root existence appears to have been realized in one case at least.

The complex and multiform aerating systems found in the aerial portions of many plants have little importance for the present inquiry.[1] In the case of green plants it is probable that these systems are occupied more with the supply of the carbon dioxide used in photosynthesis[2] than with the supply of oxygen for respira-

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[1] On these systems see: Unger,- Sitzungsber. Akad. Wiss. Wien 12: 367 (1854); Dufour,- Arb. Würzburg 3: 37 (1887); Goebel,- Bot. Ztg. 45: 717 (1887); Devaux,- Rev. gen. Bot. 3: 49 (1891), Ann. Sci. nat. (8) 12: 221 (1900); Aubert,- Rev. gen. Bot. 4: 276 (1892); Pappenheim,- Bot. Centbl. 49: 36 (1892); Bonnier,- Rev. gen. Bot. 5: 111 (1893); Hunter,- Ann. Bot. 29: 627-634 (1914). Further literature is cited by Pfeffer,- Physiology of Plants, vol. 1, pp. 176-206 (1900) and Haberlandt,- Physiological Plant Anatomy, pp. 432-484 (1914).

[2] For instance Stahl has found the aerating system better developed when plants are grown in strong light. Über den sonnigen und schattigen Standorts auf der Ausbildung der Laubblätter, 1883, p. 17. On the entry of carbon dioxide into the aerating systems see the classical investigations of Brown and Escomb,- Phil. Trans. 193: 223-292 (1900), Proc. Roy. Soc. 70; 397-413 (1902).

tion. In any case their existence in leaves and shoots means nothing as to conditions in roots or other subterranean parts. It is true, however, that air passages which appear to be continuous with the subaerial aerating system have been identified in a number of roots and are usually imagined to function as channels of oxygen supply.[1] There appears to have been no direct experimentation on the function of these air passages in roots or on the amount of oxygen which is, or can be, supplied to the deep-lying roots in this way. In the search for evidence implying the need of soil aeration the matter is not important, since the possession of an efficient internal aerating system would, in itself, make a root reasonably independent of the degree of aeration in the surrounding soil. But in connection with the problem of the nature of the root respiration it is interesting to inquire what quantity of oxygen could be supplied to roots by means of these internal aerating systems.

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[1] Hohnfeldt,- Bot. Jahresber. 1880: 48; Kohl,- Transpiration der Pflanzen, p. 26, 1886; Bancroft,- Bot. Jahresber. 1889: 49; Devaux,- Bull. Soc. Bot. 38: 48 (1891); Pfeffer,- Druck und Arbeitsleistung, p. 245 (1893); Brenner,- Ber. deut. bot. Ges. 20: 175 (1902); Warming,- Oecology, p. 44 (1909); Hunter,- Ann. Bot. 29: 627-634 (1914).

Nearly all such oxygen supply will be by diffusion. The compressions and expansions which take place in the internal air passages of aerial organs ~~under~~ during bending by the wind or other forces do not occur in roots. The diurnal temperature changes of the deeper layers of soil are both slow and slight. Changes of atmospheric pressure have been shown by Buckingham[1] to have relatively very little effect on the diffusion of oxygen and carbon dioxide into and out of soils, and the effect would be still less important in the long and narrow air passages of roots. It is probable that changes of turgor may enlarge or restrict slightly the internal air spaces and these changes may be frequent and considerable enough to have some effect. It is scarcely probable that they can approach in magnitude the effects of diffusion. Growth movements are similarly insignificant. Continuous gaseous currents such as those which have been observed in Nelumbrum and certain other plants[2] are impossible

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[1] U. S. Bureau of Soils, Bulletin 25, pp. 26-33, 41-45, 47-50 (1904).

[2] Raffenau-Delile,- Ann. sci. nat. (2) 16: 328 (1841); Lechartier,- Ann. sci. nat. (5) 8: 364 (1867); Merget,- C. R. 77: 1469 (1873), 78: 884 (1874); Bathelemy,- Ann. sci. nat. (5) 19: 152 (1874). Palladin suggests a physical explanation based on the phenomena of differential gas diffusion through heated porous plugs,- Pflanzenphysiologie, p. 123 (1911).

in roots since the root-passages form a closed system open only at one end.

At first sight it might seem that the metabolic removal of oxygen from the atmosphere of the root-passage might create an inward draft of air, provided, of course, that all the carbon dioxide produced were excreted outward into the soil and did not have to diffuse backward through the passage. This would be true if the gas supplied at the outer end of the passage were pure oxygen. But it is not. It is air, and the removal of the oxygen leaves approximately 80 percent of nitrogen. Very soon, therefore, the atmosphere within the root passage becomes nitrogen plus what oxygen can be supplied by diffusion.

The actual cases of oxygen diffusion into root passages are too complex for quantitative treatment but it is interesting to examine a simple case which is somewhat analogous. We imagine a single air passage one millimeter in diameter and one meter long. We assume that this is supplying oxygen to lower-placed root tissue only; that is, no oxygen is absorbed or otherwise removed during passage through this one meter length. We assume that the inner end of this passage communicates with a section of the root-spaces from which all the oxygen which arrives is immediately removed and that the outer end communicates with air. Temperature is assumed constant.

Physically, this is the simple case of the diffusion of one gas into another. Ignoring certain minor variations, the establishment of a "steady state" of rate of oxygen movement will see a continuous decrease of the concentration of oxygen from that of the outer air to the zero concentration at the inner end of the passage. The physical theory of the mutual diffusion of two gases in contact is applicable, with some possible exceptions which are minor and do not require attention. According to this theory[1],

$$V = Kst \frac{dp}{dx}$$

in which formula "V" is the volume of gas diffusing, expressed in cubic centimeters per second; "s" is the area across which diffusion is occurring, expressed in square centimeters; "t" is the time in seconds; $\frac{dp}{dx}$ is the rate of change of the partial pressure of the diffusing gas (which is nearly the same as the rate of change of volume concentration) expressed in atmospheres (760 mm.) per centimeter; and K is the diffusion constant or "coefficient of diffusion". This constant differs with the gases concerned and is directly proportional

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[1] See, for instance, Chwolson,- Traite de physique, vol. 1, pp. 528-529 (1908), where the original investigations are cited.

to the square of the absolute temperature and inversely proportional to the total pressure of both gases.[1] The constant for the diffusion of oxygen into nitrogen has been determined by Obermeyer[2] for 0° C. and for 760 mm. pressure, as .171. The average temperature of plant roots is probably about 20° C (293° absolute). The constant for this temperature and for atmospheric pressure (760 mm.) would be to .171 as 293° is to 273°, or .197. For the assumed case, "s" (the area of the tube) equals π times the square of the radius, or .007854 square centimeter. We take the time as one hour or 3600 seconds. The change of partial pressure (or concentration) of oxygen is from .2 atmosphere at the

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[1] These relations are approximate only but will suffice here. For details see Stefan,- Sitzungsber. Akad. Wiss., Wien, math.-naturw. kl. 63: 63 (1878); Loschmidt,- Sitzungsber. Akad. Wiss., Wien, math.-naturw. kl. 61: 367 (1870), 62: 468 (1871); Obermeyer,- Sitzungsber. Akad. Wiss., Wien, math.-naturw. kl., 85: 147, 748 (1880), 87: 188 (1881), 96: 546 (1883).

[2] *Loc. cit.*, Through Smithsonian Physical Tables, 6th ed., reprint, p. 140 (1916).

outer end[1] to 0 at the inner end, which is .2 atmosphere per 100 centimeters, or .002 atm. per cm. The total pressure is assumed constant at one atmosphere. Substituting these numerical values in the above formula we have:

$$V = .197 \times .007854 \times 3600 \times .002$$

or V = .01114 cubic centimeter per hour. Under the assumed conditions, therefore, a little over one one-hundredth of a cubic centimeter of oxygen would diffuse through a root-passage one millimeter in diameter and one meter long. It is obvious that this will not provide any large oxygen supply for the respiration of tissues lying beyond the one-meter point.

This numerical value must not be considered as having any quantitative precision or as being more than an indication of the general order of the quantity of oxygen which would diffuse. The necessary simplifying assumptions have simplified all reality out of the case. However, the value given is probably above rather than below the truth. The assumed diameter of one millimeter is unusually large for actual root-passages. It will be noted that the rate of diffusion, other things being equal, is proportional to the cross sectional area

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[1] The composition of the atmosphere is assumed to be 20 percent oxygen and 80 percent nitrogen, by volume. See page 5[illegible] , below.

of the passage, that is to the square of the diameter. Accordingly, this rate decreases rapidly as the passage becomes smaller. Furthermore the actual passages are very tortuous and frequently constricted by narrowings, small orifices of communication between vessels, etc. All of these tend to reduce the diffusion rate. The assumption of no removal of oxygen during passage through the tube is obviously untrue but is probable compensated for by the increased size of passage or by the presence of additional parallel passages in the thicker root-portions nearer the air. Of the factors other than simple diffusion, all but one can be discussed as certainly of lower order than the diffusion effect. This one is the effect of turgor changes in the root. On this matter not only is experimental data entirely lacking but there are not even materials for intelligent speculation.

Although the calculations outlined suggest that oxygen entry through the air-passages of long roots cannot be very great, it is not intended to assert that such oxygen supply is necessarily insignificant in all cases. Indeed certain specific morphological data imply the existence of a real relation between root passages and aeration in the particular cases concerned. Thus it is stated that swamp plants usually have large and more numerous internal air passages than have typical land

plants.[1] The air-spaces of some roots are said to be relatively larger toward, and in, the growing tip than in the older, less active portions.[2] Amphibious plants are reported to develop more and larger aerating systems when grown in water than on land.[3] Finally, a number of swamp plants are known to provide themselves with special organs for internal root aeration. The best known of

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[1] Goebel,- Pflanzenbiol. Schilderungen, vol. 2, p. 249 (1893); Warming,- Oecology, pp. 44, 98 (1909); Haberlandt,- Physiological Plant Anatomy, p. 441 (1914). There are, however, many exceptions; cf. Goebel,- *loc. cit.*

[2] Hunter,- Ann. Bot. 29: 627-634 (1914).

[3] Stahl,- Einf. sonnigen und schattigen Standorts, p. 17 (1883); Schenck,- Biol. der Wassergewächse, p. (1886), Jahrb. wiss. Bot. 20: 526 (1889); Goebel,- Pflanzenbiol. Schilderungen, vol. 2, pp. 255-256 (1893); Wieler,- Jahrb. wiss. Bot. 32: 519 (1898); Glück,- Wasser- und Sumpfgewächse, vol. 1, pp. 268-70, (1905). Glück (*loc. cit.*) notes that some of the modification produced by growth in water may be a response to change of light intensity rather than to aëration.

these are the pneumatophores or "breathing roots" of the mangrove but several other marsh and water plants have similar organs.[1] All of these forms are essentially alike in containing air passages or spongy tissue communicating above with the atmosphere and below with the internal air passages of the submerged root. Although there is little experimental evidence, there can be no doubt that these organs furnish a channel for the supply of oxygen to the roots and for the escape of carbon dioxide

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[1] On pneumatophores and other forms of aerenchyma see: Wiesner,- Sitzungsber. Akad. Wiss., Wien 79: (1879); Warming,- Engler's Jahrb. 4: (1883), Oecology, pp. 186, 236 (1909); Goebel,- Ber. deut. bot. Ges. 4: 1 (1886), Sitzungsber. naturf. Ges. Rostock _____: (1886), Bot. Ztg. 45: 717 (1887), Pflanzenbiol. Schilderungen, vol. 2, pp. 256-266 (1893), Organographie, vol. 2, pp. 479-481 (1901) (English edition, pp. 278-280); Scott,- Ann. Bot. 1: 306 (1886); Jost,- Bot. Ztg. _____: 601 (1887); Lietzmann,- Flora _____: (1887); Schenck,- Jahrb. wiss. Bot. 20: 526 (1889), Flora _______: 83 (1889); Schrenck,- Bull. Torrey Bot. Club 16: 315 (1889); Wilson,- Proc. Phila. Acad. Nat. Sci. _____: (1889), Bot. Centbl. 43: 148 (1890); Karsten,- Ber. deut. bot. Ges. 8: (49) (1890), Bibliotheca Bot. 22: 51 (1891); Wiesner and Molisch,- Sitzungsber. Akad. wiss., Wien, math.-naturw. kl. 98: (1890); Rosanoff,- Bot. Ztg. _______: (1891); Schimper,- Bot. Mittheil. a. d. Tropen 3: (1891);

Weisse,- Ber. deut. bot. Ges. _____: 303 (1897); von Tubeuf,- Forstl. naturw. Zeits. _______: 519 (1898); Wieler,- Jahrb. wiss. Bot. 32: 503 (1898); Börgesen and Paulsen,- Rev. gen. Bot. 12: (1900); Devaux,- Ann. sci. nat. (8): 12: 221 (1900); Westermaier,- Zur kenntnis der Pneumatophoren, (1900); Kearny,- Contrib. U. S. Nat. Herb. 5: (1901); Seliber,- Acta Leop. Carol. Acad. 84: (1905); Tansley and Fritsch,- New Phytol. 4: (1905); Witte,- Sartryck ur botaniska studier lillägnada F. R. Kjellman, pp. (1906); Koorders,- Ein von der Holländische-Indisches sumatra-Expedition endecktes Tropen-Moor, (1907); Velenovsky,- Vergleichenden Morphologie der Pflanzen, vol. 3, p. 464 (1910); Glück,- Wasser- und Sumpfgewächse, vol. 3, pp. 464, 602 (1911); Haberlandt,- Physiological Plant Anatomy, pp. 441-443, 480-482 (1914).

from them. Wieler's[1] contention that the passages are plugged and cannot serve as gas channels applies, at best, only to the case examined by him and does not weaken the conclusion that, in general, the pneumotophores are really organs of gas exchange. In the case of the mangrove and similar trees it is not improbable that gas diffusion is assisted by temperature changes causing convectional gas circulation or by expansions and contractions due to rise and fall of tides[2] (with varying external pressure on the roots) or to wind-strains communicated mechanically from the trunk.

But, while the existence of pneumatophores may be regarded as evidence of the need of aerobic root respiration on the part of the species which possess them, this evidence applies, obviously, only to those species. As a matter of fact pneumatophores of any type are rare. By far the larger number of swamp plants have neither pneumatophores or any other type of determinable organ

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[1] Jahrb. wiss. Bot. 32: 503 (1898).

[2] Westermaier,- Zur kenntnis der Pneumatophoren, p. (1900). On internal spring-like hairs which cause expansion after compression see Gürtler,- Interzell. Haarbildungen, 1905.

for root aeration. Glück[1] lists eleven species as possessing some form of root-aeration organ. These are *Lysimachia vulgaris*,[2] *L. thyrsifora*, *Lythrum salicaria*,[3] *L. graefferi*, *Lotus uliginosus*, *L. biflorus*, *Oenanthe aquatica*, *Scutellaria galericulata*, *Lycopus europaeus*,[4] *Jussiaea repens*,[5] and *J. grandiflora*. To these must be added *Aeschynomena indica*[6] and *A. hispidula*,[7] *Nesaea verticillata*,[8] *Taxodium distichum*,[9] *Carapa moluccensis*,[10],

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[1] Wasser- und Sumpfgewächse, vol. *3*, pp. 464, 602 (1911).

[2] See also Witte,- Särtryck ur bot. stud. tillägnade F. R. Kjellman, (1906).

[3] See also Goebel,- Pflanzenbiol. Schilderungen, vol. 2, p. 261 (1893).

[4] See also Goebel,- Pflanzenbiol. Schilderungen, vol. 2, p. 262 (1893).

[5] See also Seliber,- Acta Leop. Carol Acad. *84*: (1905); Velenovsky,- Vergleichende Morph. Pflanzen, vol. *2*, p. 394 (1907).

[6] Goebel,- Pflanzenbiol. Schilderungen, vol. *2*, p. 262 (1893).

[7] Ernst,- Bot. Ztg. ______: 586 (1872). For the interpretation of the mopphological data see Goebel,- Pflanzenbiol. Schilderungen, vol. 2, p. 262 (1893).

[8] Schrenk,- Bull. Torrey Bot. Club *16:* 315 (1889

[9] Kearny,- Contrib. U. S. Nat. Herb. *5:* (1901).

[10] Karsten,- Biblioteca Bot. *22*: 51 (1891).

Sesbania aculeata,[1] at least one species each of Sonneratia[2] and Desmanthus[3] and several species each of Avicennia,[4] Laguncularia,[5] Rhizophora and Jussiaea[6] (in addition to the two above noted). This makes perhaps 25 species as compared with at least several hundreds of known species of swamp plants. It is obvious that the evidence from pneumatophores means little with regard to the question of root respiration in general.

Conclusions regarding soil aeration are frequently drawn, also, from the tendency of the roots of many plants to remain in the superficial layers of

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[1] Scott,- Ann. Bot. 1: 306 (1886); Goebel,- Organographie, vol. 2, p. 481 (1901).

[2] Goebel,- Ber. deut. bot. Ges. 4: 1 (1886).

[3] Rosanoff,- Bot. Ztg. ____: (1891).

[4] Schenck,- Jahrb. wiss. Bot. 20: 534 (1889); Flora ______: 83 (1889).

[5] Scenck,- loc. cit.; Goebel- Organographie, vol. 2, p. 481 (1901).

[6] Goebel,- Pflanzenbiol. Schilderungen, vol. 2, pp. 257-260 (1893), Organographie, vol. 2, p. 481 (1901).

soil.[1] Doubtless this is true of a considerable majority of known soil-living species. Deep-rooted plants are the

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[1] On root systems and root habits see: Nobbe,- Landw. Vers. Stat. 4: 217 (1862), 10: 94 (1868), 15: 391 (1872), 18: 279 (1875); Fraas,- Wurzelleben der Culturpflanzen, 1870; Schwarz,- Unters. bot. Inst. Tübingen 1: 135 (1883); Kraus,- Forsch. Geb. Agr. Physik 12: 259 (1889), 15: 234-286 (1892), 17: 35-103 (1894), 18: 113-166 (1895), 19: 17, 80-129 (1896); King,- Wisc. Agr. Exp. Sta., Report 1892: 112-120, 1893, 160-164; Goff,- Wisc. Agr. Exp. Sta., Report 1897: 286-298; Georgeson and Payne,- Kansas Agr. Exp. Sta., Bull. 75: 212-222 (1898); Ten Eyck,- North Dakota Agr. Exp. Sta., Bull. 36: 333-346 (1899), 43: 535-550 (1900); Busgen,- Allg. Forst.- und Jagd-Ztg. 67: 273-278, 305-309 (1901); Freidenfelt,- Flora 91: 115 (1902); von Seelhorst,- Jour. Landw. 50: 91-104 (1902); Sheppard,- North Dakota Agr. Exp. Sta., Bull. 64: 525-540 (1904); Booth,- New York State Agr. Exp. Sta., Report 1907, part 3: 345-349 (1907); Rotmistrov,- Zhur. Opyt. Agron. 8: 667-705 (1907), 9: 1-24 (1908), Root System of Cultivated Plants (1909); Schulze,- Wurzelatlas, vol. 1, (1911), vol. 2, (1914), Festschrift 50 Jubiläum Agr. Chem. Versuchs u. Kontroll Stat. Breslau, pp. 67-95 (1913); Cannon,- Carnegie Inst. of Wash., Pub. 131 (1911), Pop. Sci. Mon. 81: 90-99 (1912), Science 37: (1913), Plant World 16: 323-341 (1913).

exception rather than the rule and many shallow-rooted species develop their root-systems entirely within the surface foot or eighteen inches of the soil.[1] Probably this really is due in part to the better aeration of the surface soil but it is not, in itself, evidence to that effect. For instance, Cannon[2] has shown that in some species the habit of shallow rooting is a response to differences in soil temperature. Furthermore deep-rooted plants, though not so common as those of shallow habit, are plentiful and occasional cases of extreme depth have been recorded. Thus Rotmistrov[3] says that roots of Alfalfa have been found at a depth of 70 feet (21 m.). Bessey[4] recorded roots of lupine at 60 to 70 feet (18 to 21 m.) in the dune lands near San Francisco. Hilgard

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[1] See especially Cannon,- loc. cit. (Pub. 131).

[2] Car. Inst. of Wash., Yearbook 13: 81-82, 93-96, 96-97 (1914); Science,- 41: 173-174 (1915); Amer. Jour. Bot. 2: 211-224 (1915). See also Tolsky,- Zhur. Opyt. Agron. 2: 733-744 (1901).

[3] Root Systems, p. 3 (1909).

[4] Quoted by Todd,- Proc. Amer. Asso. Adv. Sci. 27: 238 (1878).

has observed the roots of alfalfa at 25 feet (7.6 m.)[1] and mentions depths of 60 feet (18 m.) as "credibly reported". The same author records vine and fruit tree roots at 20 feet (6 m.)[2] and roots of sagebrush (Artemisia) and saltbush (Atriplex) at the same depth[3]. Hop vine roots were found at 10 feet (3 m.)[4] and roots of two native California plants (*Chenopodium californicum* and *Scrophularia californica*) at 11 feet 2 inches (3.4 m.) and 10 feet 6 inches (3.2 m.), respectively[5]. Cannon has observed roots of mesquite (*Prosopis velutina*) at 5 m. and mentions them as reported at 8 m.[6] Many desert perennials

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[1] Soils, p. 229 (1906).

[2] l.c., p. 231.

[3] l.c., p. 230.

[4] l.c., pp. 171-172.

[5] Hilgard,- Soils, pp. 173-174 (1906).

[6] Car. Inst. of Wash., Pub. 131, pp. 80, 92 (1911); Car. Inst. of Wash., Yearbook, 12: 72 (1913).

may extend their roots to depths of from 2 to 5 meters.[1] Goff[2] reports grape roots at 13 feet (4.1 m.) and roots of a seven-year-old apple tree at 9 feet (2.7 m.). Corn roots are reported at 7 feet (2.1 m.) by King[3] and by Georgeson and Payne[4]. The latter authors report the roots of cow-pea at 6 feet (1.8 m.)[5]. According to

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[1] Cannon,- Car. Inst. of Wash., Yearbook 9: 62 (1910); Car. Inst. of Wash., Pub. 131, pp. 60, 75, 77, 80, 81, 82, 92 (1911). On deep roots of desert plants see: Volkens,- Flora der ägypt.-arab. Wüste, pp. (1887); Aitchinson,- Trans. Linn. Soc. (2) 3: (1887); Schinz,- Coloniales Jahrb. 6: (1893); Warming,- Oecology, pp. 117-118 (1909); Cannon,- Car. Inst. of Wash., Yearbook, 10: 61 (1911). On deep roots of dune plants see Warming *loc. cit. supra* and Vid. Meddel. naturh. For., Kjöbenhavn ______: (1891).

[2] Wisc. Agr. Exp. Sta., Report 1897: 286-298.

[3] Wisc. Agr. Exp. Sta., Report 1891: 131-134.

[4] Kans. Agr. Exp. Sta., Bull. 75: 212-222 (1898).

[5] *loc. cit.*

Alway[1] cereal roots may reach 7 feet in Saskatchewan. Pfeffer records roots of clover and of Lathyrus sylvestris at 2 to 3 meters.[2] Again, the roots which are able to penetrate deeply into water-saturated soils certainly cannot receive important supplies of atmospheric oxygen, regardless of the actual depths at which they lie.

Direct evidence as to root respiration and aeration might be obtained, perhaps, from a systematic study of the composition of the gases present in the root passages. However, the information now available is not sufficient for any conclusions. The internal air of several roots has been analyzed by Dutrochet,[3] Heintz,[4] and Devaux.[5] All found the carbon dioxide content higher and the oxygen content lower than in the open atmosphere or in the ordinary soil air. As might be expected there is great individual variation. The same enrichment in

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[1] Quoted by Hilgard, Soils, p. 171 (1906).

[2] Physiol. of Plants, vol. 1, p. 153 (1900).

[3] Memoires, etc., p. 175 (1837).

[4] Ber. chem. Ges. 6: 670 (1873).

[5] Ann. sci. nat. (7) 14: 352 (1891); Rev. gen. bot. 3: 49 (1891).

carbon dioxide and depletion in oxygen has been found by Bender in the inner air of apples.[1] The data of the composition of the inner air of wood, leaves and other subaerial parts ~~is~~ are conflicting.[2] Sometimes it is enriched in oxygen, sometimes in carbon dioxide. This is to be expected, since the composition of this inner air will depend upon the balance between respiration and photo-

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[1] Ber. chem. Ges. 8: 112 (1875).

[2] Ingenhousz,- Versuche mit Pflanzen, vol. 2, p. 58 (1788); Saussure,- Ann. chim. phys. 19: 150 (1821); Calvert and Ferrand,- Ann. sci. nat. (3) 3: 377 (1844); Gardner,- Froriep's neue Notizen 39: 323 (1846); Schülze,- Lehrb. Chem. f. Landw., vol. 1, p. 58 (1853); Erdmann,- Jahresber. Chem. 1855: 727; Baudrimont,- C. R. 41: 178 (1855); Martin, C. R. 62: 737 (1866); Faivre and Dupre,- Ann. sci. nat. (5) 6: 366 (1866); Barthelemy,- Ann. sci. nay. (5) 19: 167 (1874); Saintpierre and Magnien,- C. R. 83: 490 (1876); Boehm,- Landw. Vers. Stat. 21: 373 (1878); Joulin,- Bot. Centbl. 5: 102 (1881); Grehoult and Peyrou,- C. R. 100: 1475 (1885); Peyrou,- C. R. 101; 1023 (1885), Bot. Centbl. 45: 217 (1891); Kruticki,- Bot. Centbl. 39: 30 (1889); Devaux,- Ann. sci. nat. (7) 14: 297 (1891); Aubert,- Rev. gen. Bot. 4: 275 (1892).

synthesis and will vary, therefore, with the condition of the plant, the time of day, and the intensity of light. Data as to the inner air of water plants is similarly conflicting[1] and for similar reasons.

The cultural evidence suggesting the necessity of soil aeration would be better described by saying that it suggests the unsuitability of soils which are water-logged. The extreme case is that of swamp soils which are inhospitable to most dry-land plants though possessing a rich special flora of their own. Of important agricultural plants only rice, asparagus and the cranberry will grow successfully on such soils. Less extreme cases of bad drainage and high water-table are common everywhere and such soils are almost always below normal in productivity. It is the usual assumption that the bad results of insufficient soil drainage are due largely if not entirely, to inadequate aeration.[2]

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[1] Aime,- Ann. sci. nat. (3) 2: 536 (1841); Devaux,- Ann. sci. nat. (7) 9: 35 (1889); Wille,- Bot. Jahresbar. 1889: 226; Loven,- Svensk. Vet. Akad. Handl., Bihang. 17: (1891); Aubert,- Rev. gen. bot. 4: 275 (1892).

[2] Wollny,- Exp. Sta. Rec. 3: 533, 536-537, 541-542 (1892), Forsch. Geb. Agr. Physik 20: 52 (1897), Fühling's Landw. Ztg. 48: 377-382, 401-405, 441-445 (1899); Mangin,- C. R. 120: 1065-1068 (1895), Ann. soc. Agron. (2) 1: 1-68 (1896); Walker,- Jahrb. wiss. Bot. 32: 71

(1898); Lee,- Queensland Agr. Jour. 11: 50-52 (1902); Warming,- Oecology, p. 43 (1909); Beinback,- Forstw. Centbl. 36: 26-44 (1914); Stookey and Stookey,- Wash. Agr. Exp. Sta., Mon. Bull. W. Wash. Substa. 1, No. 7 (1914).

Similarly the effect of rolling in compacting the soil has resulted in an injury ascribed to decreased aeration[1] and the injury to forests through accumulation of vegetable refuse on the soil has been referred to decrease in the ease of renewal of the soil air.[2] Similarly Hesselman[3] ascribes the death of certain pine forests by "swamping", not so much to excess of water as to deficient aeration. He reports that running water, which is well aerated, does not kill the trees even when it stands above the soil surface. Graves[4] has assigned to deficient soil aeration a case of root-rot in conifers growing in impervious soil and Elst[5] has described a root-rot disease of rice which he believes due, in part at least, to poor soil aeration.

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[1] von Seelhorst and Krzymowski,- Jour. Landw. 53: 269-278 (1905).

[2] Hartig,- Textbook of diseases of trees, pp. 276-278 (1894).

[3] Meddel. Stat. Skogsförsöksanst. 1910, No. 7, pp. 91-125.

[4] Phytopath. 5: 213-217 (1915).

[5] van. der Elst,- Dept. Landb. Nijv. en Handel, Meded Proefstat. Rijst., 104 pp. (1912).

Howard and Howard[1] have attributed to aeration difficulties the "wilt disease" of Java indigo and certain other agricultural difficulties encountered on the heavier and better-watered soils of India. These authors also refer to disturbances of aeration the toxic effect of grasses on trees under which they grow.[2] MacDougal[3] suggests that poor aeration due to puddling of the soil while under water may explain the slowness with which plants are establishing themselves on the beaches now emerging from ten years submergence by the Salton Sea. On the other hand, the benefits of good drainage, looser texture and the like are frequently ascribed to improved aeration[4]. Soil improvement by earthworms has been referred to the effect of their burrows in increasing aeration.[5]

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1. Agr. Res. Inst. Pusa (India), Bull. 52: 35 pp. 1915.

2. On this toxic effect see Pickering and the Duke of Bedford,- Jour. Agr. Sci. 6: 157 (1914), and Russell,- Soil Conditions and Plant Growth, 2nd ed., pp. 113-116 (1915).

3. Geog. Review 2: (1917).

4. See authors cited on page 41 , note , especially the articles of Wollny.

5. Wollny, Forsch. Geb. Agr. Phys. ____: 382 (1890); Djemil,- Ber. Physiol. Lab., Vers. Sta. Halle ____: (1898); Friend,- Sci. Prog. 6: 393-401 (1912).

It is important to realize that the explanation of these various effects, injurious and beneficial, by reference to changes of aeration is entirely hypothetical. Too much water in the soil, a texture which is too compact, and the like are injurious to plants. They also decrease the ease and degree of soil aeration. It is pure assumption to say that the injury is due to the decreased aeration. This assumption is probably true but it cannot be accepted on the basis of evidence which is to entirely inferential. The soil conditions which control plant health are complex. Deficient drainage or excessive compacting will alter not only the air- supply of the soil but also its water supply, the nature and number of the microflora and fauna, the chemical reactions occurring (as, e.g., through adsorption or catalysis), the mechanical ease or difficulty of the penetration of roots, and possibly still other factors. Any or all of these may affect the plant growth or behavior quite as importantly as the supply of air to the roots.

The published cultural experiments on soil aeration are marred by similar failure to take into account the real complexity of the conditions. Thus

Stone and Monahan,[1] Day,[2] and Hunter[3] have made experiments on the effect of forcing air through soil in which plants were growing. The results are inconclusive and vary for different plants and for different experiments. This is to be expected from a consideraiton of the many ways in which such a procedure might alter the soil. Probably the disturbance of water relations alone would account for the variability of the results. The same uncertainty applies to the experiments of Biesenbach[4] and Causemann[5] who planted trees in holes partly filled with brushwood and other loose material, which was supposed to facilitate aeration. No doubt aeration was facilitated but it is probable that change in ~~of~~ water relations and the supply of organic matter were more important. It has

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[1] Mass. Agr. Exp. Sta., Report 1905: 115-145.

[2] Ontario Agr. Coll. and Exp. Farm, Report 31: 37-40 (1905), 32: 30-37 (1906).

[3] Proc. Univ. Durham Phil. Soc. 4: 183-186 (1911-1912). For incidental experiments of Cannon see Cannon and Free,- Science 45: 178 (1917). The similar experiments of Noyes and others with carbon dioxide will be discussed below (pages 52-54).

[4] Deut. landw. Presse 30: 752 (1903).

[5] Deut. landw. Presse 31: 619-620 (1904).

been observed by Parr[1] and Friedersdorff[2] that crops on drained land are improved by opening both ends of the tile-drain lines to the atmosphere, thus increasing air circulation in the drain-pipe. This improvement may be due to increased soil aeration but such a relation is not immediately obvious. Indeed Mitscherlich[3] has pointed out that soil-aeration is not likely to be increased very greatly for the reason that the drain-tile is usually wet and impermeable to gases except by solution in, and diffusion through, the pore-water of the tile.

If there is uncertainty as to the real cause of the cultural benefits usually ascribed to soil aeration, there is still less reason to regard this evidence as importantly supporting the usual assumption of the need of aerobic root respiration. It is quite possible that adequate soil aeration might be a cultural necessity even though all roots were fully capable of anaerobic respiration. Among the most important reactions of the soil on plant life are those due to the chemical nature of the soil solution and those due to the nature of the microflora and fauna of the soil.

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[1] Agr. Jour. India 7: 371-372 (1912).

[2] Deut. landw. Presse 39: 483-485, 493-498 (1912).

[3] Bodenkunde, 2nd ed. p. 248 (1913).

It is difficult to separate these two factors, since they react importantly on each other, but it is certain that the degree of soil aeration has great importance to both. Under conditions of poor aeration, however caused, various reduction reactions occur in the soil and lead to the formation of ferrous salts, hydrogen sulphide and other compounds[1] which are toxic to most plants. Probably these reductions themselves are due largely to anaerobic bacteria[2], but many other changes in the micro-organisms of the soil follow extreme decreases in soil aeration. Thus the organisms responsible for nitrification in the soil are largely aerobic, while the denitrifyers are in part anaerobic.[3]

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[1] Hilgard,- Soils, pp. 18-19, 45-46, 75-76, 231-233 (1906); Gamble and Slater,- Ontario Dept. Agr., Bull. 178, 39 pp. (1909).

[2] Beijerinck,- Centbl. Bakt., _____: (1895); van Delden,- Centbl. Bakt. 11: (1903); Kossowicz,- Bodenbakt., pp. 11-15, 54-74 (1912); von Wolzogen-Kühn,- Arch. Suikerind. Nederland. Indië 23: 501-511 (1915); Lipman in Marshall,- Microbiol., pp. 358-362 (1917).

[3] See the works on soil bacteria referred to below (page 45 , note 1) also: Krüger,- Ein Beitrag zur Untersuchung der Stickstoffumsetzung im Boden, Inaug. Diss., Königsberg. 1908.

It is obvious that aeration will effect importantly the nitrogen cycle in the soil. Doubtless additional effects follow the encouragement of putrifactive and other anaerobic organisms by deficient aeration.[1] These may be expecially important in the complex reactions involved in humus formation.[2] The toxins which are probably excreted by higher plants under anaerobic conditions have already been mentioned.[3]

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[1] On putrifaction and fermentation in soils see: Kossowicz, loc. cit.; Sorauer,- Handbuch Pflanzen krankh. vol. 1, pp. (1886); Wacker,- Jahrb. wiss. Bot. 32: 71-116 (1898). On toxic excreta of bacteria see Dandeno,- Report Mich. Acad. Sci. 10: 32-36 (1908).

[2] See Wollny,- Jour. Landw. 34: 213-230 (1886), Der Zersetzung der organischen Stoffe, pp. 140ff, (1897); Sjollema and de Ruijter de Wildt,- Verslag Landbouwk Onderzoek. Rijkslandbouw proefstat 1: 21-68 (1907), 7: 106-146 (1910). On soil bacteria in general see Kossowicz,- loc. cit.; Löhnis,- Handb. landw. Bakteriol. (1910); Russell,- Soil Conds. and Plant Growth, 2nd ed., pp. 117-139 (1915); Lipman in Marshall,- Microbiology, 2nd ed., pp. 289-363 (1917).

[3] See pages 18-21 and literature cited on page 19, note 1

These chemical and micro-organic effects which follow decrease in soil aeration have been investigated only very superficially and are too little known for detailed analysis. It is manifest, however, that the effects of soil aeration on the plant may be secondary as well as primary and that the fact that bad aeration is injurious and good aeration beneficial, does not necessarily mean anything as to the aerobic or anaerobic character of root respiration. Even the observed good and bad effects of good and bad aeration may be complicated by the effects of the other factors which are changed, purposely or accidentally, at the same time that the aeration is changed.

It is interesting that the number of bacteria in the soil increases down to a depth of about one half meter, below which it decreases again.[1] Very few bacteria are found below 3 meters in agricultural soils. This distribution of the bacteria may be a response to aeration but it is equally possible that it is caused by the supply of organic food. Nothing is known concerning the

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[1] Fraenkel,- Zeits. für Hyg. 5: 332 (1889); Hilgard,- Soils, pp. 145, 282; Warming,- Oecology, p. 79 (1909).

effect of aeration on the protozoa, nematodes, fungi, algae and other non-baterial organisms of the soil,[1] but it is probable that most of them are aerobic and perish or pass into resting stages when aeration is deficient. Whether these changes are, as a rule, beneficial or injurious to higher plants it is impossible to say.

In connection with the un$\overset{c}{d}$ertainties as to the cause and even the reality of the effect of soil aeration on plants it is interesting to note that a similar conflict of evidence occurs in the matter of the aeration of the nutrient solution when plants are grown in water-cultures. Aeration of the solution (by shaking or by blowing air through it) has been found beneficial by Wilms,[2] Aiker,[3] Ehrenberg,[4] and Underwood[5] and some

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[1] On protozoa see Koch,- Jour. Agr. Res. 4: 511-559(1915). On nematodes see Cobb,- U. S. Dept. of Agr., Yearbook 1914: 457-490 (1915). On fungi see Waksman,- Soil Science 2: 103-155 (1916).

[2] Jour. Landw. 47: 261 (1899).

[3] Inaug. Diss., Erlangen, p. 72 (1900).

[4] Zeits. für Pflanzen Krankh. 16: 193 (1905).

[5] Hall, Brenchley and Underwood,- Phil. Trans. Roy. Soc. (London), B, 204: 179-200 (1913).

procedure for aeration is embodied in most directions for water-cultures and is usually employed.[1] This general opinion is re-inforced by the observation of Kosaroff[2] that the passing of a stream of hydrogen through the culture solution decreased the absorption of water by plants of Phaseolus multiflorus. On the other hand Pember[3] has found that the passage of a stream of air through the culture solution has no effect on the growth of barley and Free[4] has obtained similar negative results with buckwheat, the passage of streams of air, nitrogen and oxygen being alike without determinable effect on the growth rate or the total production of dry matter. It seems probable that the effect of aeration in water-cultures, as in soil, is complex and varies with the individual nature and circumstances of each culture. The effect of carbon dioxide in water culture will be discussed on page 83 below.

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[1] See Pfeffer,- Physiology of Plants, vol. 1, p. 420 (1900); Ehrenberg,- Bodenkolloide, p. 516 (1915). For an excellent review of the literature of work with water-cultures see Tottingham,- Physiol. Res. 1: 138-159 (1914).

[2] Diss., Leipzig, pp. 51-57 (1897).

[3] Rhode Island Agr. Exp. Sta., Bull. 169: pp. 24-25 (1917).

[4] Johns Hopkins Univ., Circular ______: (1917).

The inferential evidence concerning the need of soil aeration and of aerobic root respiration which has been discussed in this chapter may now be summarized. It should be noted that there are two subjects of inquiry - soil aeration and root respiration - and that they are not necessarily the same. Even were anaerobic root respiration always possible, adequate soil aeration might be necessary in order to prevent injurious reaction on the soil micro-organisms or the formation of injurious chemical compounds. On the other hand, aerobic root respiration might be a universal necessity and soil aeration nevertheless unimportant, because of the natural aeration of soils being always sufficient for the needs of the roots.[1]

The evidence concerning root respiration is: (1) analogy with other plant organs, (2) the experimental discovery of normal, aerobic respiration in the case of certain roots, and (3) the possession ~~of~~ by certain roots of special morphological arrangements apparently adapted to facilitate aeration. The argument by analogy is worthless since many organisms can respire anaerobically for indefinite periods and most organisms appear to be able to do so for a limited time. Similarly the observation of aerobic respiration in roots does not prove anaerobic respiration impossible, even for those particular roots,

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[1] This has been urged by Mitscherlich,- Bodenkunde, 2nd ed., p. 151 (1913).

since numerous organisms are facultative anaerobes and can respire either way. The existence of special organs for root respiration is strong evidence in favor of the need of aerobic respiration on the part of the roots of species which possess such organs, but means nothing as to the nature of root respiration in the much more numerous species in which special aerating organs are lacking.

The evidence as to soil aeration is essentially that most plants appear to grow better under conditions of moderate water content in the soil and moderate oppenness of soil texture, which conditions are also favorable, or are believed to be favorable, to soil aeration. The conclusion of the cultural benefits of soil aeration is probably true but this particular argument in favor of it is of little weight. Many other factors besides soil aeration differ in the so-called "well-aerated" and "poorly-aerated" soils. To ascribe, a priori, the cultural results to soil aeration only, is to ignore more than half of the problem. It may be agreed, however, that the growth of anaerobic organisms and the accumulation of intermediate respiration products, which result, immediately, from bad aeration and, ultimately, from excess of water, produce, in themselves, unfavorable ("toxic") soil conditions. It appears, however, that plants vary greatly in their power to withstand these toxic conditions and that soils vary similarly in their power of neutralizing or removing the toxins, even in the absence of oxygen.

In conclusion, It is probable that the roots of some plants do, and must, respire aerobically. It is probable that good soil aeration is generally beneficial, both directly and indirectly. There is no evidence indicating that these rules are absolutely general. Indeed, it is probable, by analogy at least, that some plant roots can live anaerobically and that some soils are more favorable than others to such anaerobic existence.

THE COMPOSITION OF THE SOIL AIR.

It was pointed out in the Introduction that there were two ways of experimental attack on the problems of soil aeration and root respiration; first, by analysis of actual soil air; second, by experimental study of the respiratory behavior of roots. The errors inherent in the sampling of the soil air are considerable, especially when it is desired to draw it from considerable depths in undisturbed soil or from other situations where anaerobiosis of roots is to be expected, if anywhere. For this reason the analysis of soil air does not seem the most promising line of attack on the problem and was not employed in the present investigation. It will be interesting, nevertheless, to review briefly the available data as to its composition. This data involves two things, the results of actual analyses and more general considerations (experimental and theoretical) concerning the causes which modify the soil air and determine its composition.

The first extensive investigation of the composition of the soil air was that of Boussingault and Lewy.[1] In analyses of air from fourteen soils these investigators found oxygen contents between 10.35 and 20.03 percent, carbon dioxide contents between 0.72

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[1] Ann. Chim. phys. 47: 5-50 (1853); Boussingault,- Agronomie, vol. 2, pp. 68ff. (1855).

and 0.74 percent, and nitrogen contents between 78.80 and 80.24 percent. All figures are in volume-percent. The atmospheric air at the same time and place was found to contain 20.95 percent oxygen, 79.03 percent nitrogen, and .025 percent carbon dioxide.[1] In these observations the highest contents of carbon dioxide in the soil air were found in compost material or in soils which had been recently ~~measured~~ manured. However a content of 1.79 percent carbon dioxide was found in the air from the soil of a pasture and several samples from cultivated soils ran over one percent. In general the nitrogen remains approximately constant, the oxygen and carbon dioxide rising and falling reciprocally.

The first analyses of soil air from different depths were made by Pettenkofer[2], who determined the percentage of carbon dioxide in air samples from 1.5 m. and from 4.0 m. deep. Air from the lesser depth carried .243 to 1.198 percent; that from the greater depth car-

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[1] The average composition of the atmosphere by volume is oxygen = 20.941 percent, nitrogen = 78.122 percent. The carbon dioxide is more variable. The normal is about .03 percent. It seldom falls below .025 percent or rises above .035 percent, unless in case of exceptional polution by smoke or the like. See Clarke,- Data of Geochemistry, 3rd ed., U. S. Geol. Survey, Bull. 616, pp. 41-47, where other literature is cited.

[2] Neue Rep. Pharm. 21: 677-702 (1873).

ried .346 to 2.611 percent. Similar experiments were made by Fleck[1] who found the percentages of carbon dioxide at 2, 4 and 6 meters in a soil without plant cover to be 1.68, 2.75 and 3.38 respectively. The corresponding percentages of oxygen were 18.9, 17.3 and 16.7. In soil with plant cover the conditions were reversed and the largest percentages of carbon dioxide were found in the upper layers of the soil. The experiments of Salger[2] led to results essentially similar and showed that the drawing of air from the soil for a day preparatory to taking the sample lowered the carbon dioxide content considerably in the case of air drawn from 1.5 m. but only slightly in the case of air from 3.0 m. Salger obtained carbon dioxide contents, without prior ventilation, of .39 to 1.53 percent, the high values being due, probably, to the proxemity of a refuse-pit. Experiments of Fodor[3] gave extreme values for carbon dioxide of .899 and 1.039 percent in air from 1 m. and 2.631 and 5.445 percent in air from 4 m. The corresponding oxygen values were 18.797 and 21.335 percent for 1 m. and 17.290 and 18.532 percent for 3 meters.

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1. Jahresber. Agr.-Chem. 16: 159 ( ).
2. Diss., Erlangen, 1880.
3. Boden und Wasser, pp. 99-142 (1882).

Of later experiments there need be mentioned specifically only the work of Ebermayer[1], Lau[2] and Russell and Appleyard[3]. The results of these investigators show that the percentage of carbon dioxide is higher in plant-covered soils than in bare soils, and, in general, is higher in cultivated soils than in uncultivated ones. It is also higher in summer than in winter. Much other data which need not be cited in detail is essentially confirmatory of the conclusions already stated[4].

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1. Forsch. Geb. Agr. Phys. 13: 15-49 (1890).

2. Diss., Rostock, 1906.

3. Jour. Agr. Sci. 7: 1-45 (1915).

4. For this data see: Peters,- Landw. Vers. Stat. 4: 133 (1862); Schlösing,- C. R. 77: 203 (1873); Ebermayer,- Forsch. Geb. Agr. Physik 1: 159 (1878), 3: 1 (1880); Möller,- Mitteil. forstl. Versuchswesen Oesterr. 2: 121 (1878), Forsch. Geb. Agr. Physik. 2: 329 (1879); Wollny,- Landw. Vers. Stat. 25: 373-391 (1880), Forsch. Geb. Agr. Physik 3: 8 (1880), 9: 185 (1886), 12: 385 (1889), 13: 143 (1890), 19: 151-171 (1896); Sachsse,- Lehrb. Agriculturchem., p. 142 (1888); Schloessing,- C. R. 109: 618-620, 673-676 (1889); Deherain,- Ann. Agron. 22: 449-469 (1896); Belz, in Buckingham,- U. S. Bur. Soils, Bull. 25, p. 39 (1904); Stoklasa and Ernest,- Centbl. Bakt., Abt. 2, 14: 723-736 (1905), Zeits. Zuckering Böhmen 31: 291-307 (1907); Vageler,- Mitth. Kgl. Bayerischen Moorkulturanstalt 1: 30 (1907); Barakov,- Zhur.

Opyt. Agron. 11: 321-343 (1910); Suprunenko,- Zap. Novo-Alex. Inst. Selsk. Khoz. i Liesov. 21: 59-63 (1910); Jonkov,- Khoziaistvo 6: 37-46 (1911); Zhukov,- Zhur. Opyt. Agron. 12: 552 (1911); Jodidi,- Landw. Vers. Stat. 85: 359-391 (1914); Vernadskii,- Pedogie 15: 1-21 (1914); Leather,- Jour. Agr. Sci. 7: 240-241 (1915).

In brief these conclusions are that the content of carbon dioxide is higher in soils in which active plant growth is occurring and especially where the plant cover is thick and during the season of most active growth, usually the summer. In general it is higher in soils containing much organic matter or recently manured with organic fertilizers. The content of carbon dioxide increases with depth, except in soils with very actively growing plant-cover, in which cases the carbon dioxide content may show a slight maximum 10 to 50 centimeters below the surface. The actual percentage of carbon present may vary between wide limits. In normal soils, down to 2 meters, it is seldom less than .2 percent or over 3.0 percent. The oxygen varies, in all cases, reciprocally with the carbon dioxide. When the carbon dioxide is high the oxygen is low. Actual percentages may vary from 15 to 20 percent. Even less than 15 percent may be found in very deep soils or soils possessing active plant or bacterial growth. The nitrogen is comparatively constant, usually being between 79 and 80 percent.

It is obvious that the facts of the composition of the soil air are the result of the consumption of oxygen and the production of carbon dioxide by the plant roots, bacteria and other organisms in the

soil.[1] These processes go on together, hence when carbon dioxide is high oxygen is low. Production of carbon dioxide and its content in the soil air is greatest at those times and places when and where conditions are most favorable to vital activity. Carbon dioxide ~~found~~ formed deep in the soil diffuses out more slowly, hence its percentage is higher there than in the upper layers.

In the light of the probable production of carbon dioxide and consumption of oxygen in the deeper soil layers, and of the relative slowness with which outward diffusion must remove the one and renew the other, it is a little surprising that the analyses of

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[1] Schlösing and Müntz,- C. R. 84: 301, 85: 1018 (1877); Smolenski,- Zeits. für Biol. 13: 383 (1877); Wollny,- Jour. Landw. 34: 213 (1886), Forsch. Geb. Agr. Physik 13: 143 (1890), Zersetzung organ. Stoffe, p. 122 (1897); Ebermayer,- Forsch. Geb. Agr. Physik 13: 41 (1890); Magnin,- Ann. sci. agron. 2: 1-68 (1896); Marr,- Meded. Proefstat. Oost-Java (4) 38: 503-542 (1908); Stoklasa,- Zeits Landw. Versuchsw. Oesterr. 14: 1243-1279 (1911); Hutchinson,- Report Agr. Res. Inst., Pusa (India) 1911-1912: 78-83; Haselhoff,- Landw. Jahrb. 47: 345-369 (1914); Ehrenberg,- Bodenkolloide, pp. 515-517 (1915). On the excretion of carbon dioxide by the roots of higher plants see literature cited on page 5, note 1.

air from deep in the soil show as much oxygen as they do. It is possible that the samples have been contaminated by downward leakage of atmospheric air, for instance, along the outside of the tube used for withdrawing the sample, but, in any case, the data are not sufficiently numerous to warrant any general conclusions, even if they could be regarded as sufficiently accurate.

In connection with the data of composition of the soil air it is necessary to devote a word to the total amount of air in the soil since this, jointly with the oxygen content, will determine the total amount of oxygen available to plant roots. In the simple theoretical case of an assemblage of spherical particles all of the same size, the percentage of pore space, by volume, may vary between 29.95 and 47.64[1] depending on the "packing" or mutual arrangement of the spheres. The percentage of pore space is independent of the size of the spheres though the mean diameter of the individual pore spaces decreases as the spheres are smaller. In the actual soil the particles are not spherical nor are they all of the same size, with the result that the limits of pore space given above are widened greatly. The presence of particles of various sizes tends to decrease the percentage of pore space. Thus the ad-

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[1] Schlichter,- U. S. Geol. Survey, Ann. Rep. 19: II: 306ff (1899). See also Soyka,- Forsch. Geb. Agr. Physik _____: 1 (1885).

dition of a second set of spheres of such diameter as will just fit into the pore spaces between a larger set will reduce the minimum percentage of pore space (that for closest packing) from 25.95 to 6.76. A third, still smaller set of spheres introduced into the pore spaces between those of the second set will decrease the pore space percentage to 1.76.[1] On the other hand, irregularities in the shape of the particles will tend to increase the possible pore space and this tendency is greatly increased by the flocculation and loosening of texture which is caused and maintained by the capillary water of the soil and the surface-tension forces which the capillary water system puts into action.[2]

The result of this widening of limits is that the pore space of actual soils may vary between 60 or 70 percent for soils high in organic matter to 10 percent for closely packed sands. The pore space of ordinary cultivated soils is usually between 35 and

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[1] Soyka,- Forsch. Geb. Agr. Physic _____: 1 (1885).

[2] I have discussed these matters elsewhere in detail. See Free,- Jour. Frank. Inst. 170: 21-26 (1910), Studies in Soil Physics, pp. 3-8 (1912); where further literature is cited.

50 percent.[1]

It must not be forgotten however that the entire pore space of the soil is full of air only seldom, if at all. An essential part of normal soils is the system of water films and filaments around and between the soil grains[2] and the space occupied by this capillary water system must be deducted from the total pore space in order to determine the space available for air. The amount of water-filled space will vary, according to the water content of the soil, from nearly 100 percent of the total pore space, in saturated soils, to perhaps five percent of it, or less, in soils which are entirely air-dry. Since the amount and arrangement of the capillary water system itself reacts on the arrangement of the solid soil-particles (as noted above), the actual relations between water-filled pore space and air-filled pore space will be exceedingly complex.

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[1] Hilgard,- Soils, p. 108 (1906). For measurements of percentage of pore space see Boussingault and Lewy,- Ann. chim. phys. 37: 1-50 (1853); Wollny,- Forsch. Geb. Agr. Physik 8: 368-370 (1885); Ramann,- Forsch. Geb. Agr. Physik 11: 303-308 (1888).

[2] See Briggs,- U. S. Bureau of Soils, Bull. 10 (1897); Cameron and Gallagher,- U. S. Bureau of Soils, Bull. 50 (1907); Free,- Studies in Soil Physics, pp. 3-8, 10-15 (1912).

An idea of the probable magnitude of the percentages concerned in the case of normal soils can be obtained from the following data of Russell.[1] Percentages are by volume.

	Percentage of pore space	Percentage of air	
		In normal, moist condition	After period of drouth
	Percent	Percent	Percent
Heavy loam (poor)	34.1	10.9	17.1
Arable soil, (heavily manured)	38.2	7.9	18.2
Pasture soil	47.3	7.3	25.0

It has been noted above that the actual composition of the soil air is the result of the balance between the rate at which oxygen is consumed and carbon dioxide produced by living matter and the opposing rates at which oxygen can move inward from the atmosphere and carbon dioxide can move outward, or be disposed of otherwise. The most important investigations on the gas exchange between the soil and the atmosphere are those of Buckingham.[2] As the result of careful investigations, both theoretical and experimental, this author concludes that the movement of gases in the soil follows essentially the laws for diffusion in

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[1] Soil conditions and plant growth, p. 106 (1905).

[2] U. S. Bureau of Soils, Bull. 25, 52 p. (1904).

a free space equal in volume to the pore space of the soil. It was found that the rate of escape of carbon dioxide from the soil by diffusion is equal to its rate of free diffusion in air multiplied by the square of the porosity, the porosity being expressed as the decimal fraction of space occupied by air; thus, a porosity of 50 percent is expressed as .5. The method of calculating the free diffusion of gases has been explained above (pages 26-28). Investigations of the penetration into the soil of pressure waves resulting from changes of atmospheric pressure showed that these were relatively unimportant in altering the composition of the soil air, having, at most, an effect one-twentieth as great as the effect of simple diffusion.[1] Buckingham gives a table[2] of the rates of escape of carbon dioxide and entry of oxygen, by diffusion, for soil porosities of .2 to .7 (20 to 70 percent) and concentration gradients of the diffusing gases between .1 percent per inch and 1.0 percent per inch. All percentages are by volume. The values, expressed as cubic feet per day per square foot of soil surface vary from .0082 cubic foot for a concentration gradient of .1 percent per inch ~~at~~ and a porosity of .2, and .10 cubic foot for the

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[1] On penetration of pressure-waves into the soil see also Börnstein,- Physik, Zeits. 12: 771-776 (1911)

[2] *loc. cit.*, page 38.

same concentration and a porosity of .7; to .082 cubic foot and 1.01 cubic feet for a concentration gradient of 1.0 percent per inch and porosities of .2 and .7, respectively. Calculations for two actual cases, on analytical data by Belz, gave, respectively, .10 to .15 and about .04 cubic foot of carbon dioxide escaping per day from one square foot of soil surface.[1] It should be noted that the diffusion of carbon dioxide and of oxygen in the soil is not given exactly by the diffusion coefficient for these gases diffusing into each other. In the soil they are diffusing, side by side but in opposite directions, through an atmosphere of about 79 percent of nitrogen. This alters the rate of diffusion, but the alteration can be predicted by the theory of Stefan[2] and is found to be approximately 1.12 times the rate of diffusion of carbon dioxide and oxygen without the nitrogen. This correction is taken into account by Buckingham, whose paper may be consulted for details. The similar disturbances due to the presence of water vapor are much smaller and may be neglected. The conclusion that the carbon dioxide and oxygen diffuse at nearly equal rates follows from theory and is indicated,

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[1] loc. cit., page .

[2] Sitzungsber. Akad. Wiss., Wien, math.-naturw. kl., 63: 63 ( ).

also, by the fact that the nitrogen content of the soil air remains approximately constant.[1]

Although the investigations of Buckingham are satisfactorily final with regard to the effects of diffusion and of atmospheric pressure on the composition of the soil air it would be a mistake to assume that the rates of gas exchange in the soil are limited by the values which he obtains. There are at least two other factors of importance in assisting the ventilation of the soil, namely, temperature changes and movements of the soil water. It is probable that temperature changes are less important than are usually believed. Changes in air temperature have no effect except as they alter atmospheric pressure, and such effects have been shown by Buckingham to be slight. Differences in the temperature of soil and of air may set up convectional circulations if the soil is the warmer, but it is improbable that such circulations would extend more than a few inches into the soil. More general circulations are conceivable where a hillside soil has a temperature substantially different from the temperature of the air. In such cases convectional circulations through the soil up or down the slope might occur. It is unlikely, however, that the conditions necessary for such circulation are often realized. Local extreme variations of temperature

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[1] See page 57 , above.

of soil or air, or of atmospheric pressure, as, for instance, by wind eddies, may be locally or momentarily important but can scarcely have general significance.

Next to diffusion, and perhaps even more important than diffusion, as a cause of soil ventilation are the air movements due to movements in the soil water. It is obvious that the flooding and draining of a soil will first displace the soil air and then renew it with fresh air drawn from the atmosphere. This same action occurs on a lesser scale every time the soil is wetted or dried. The nature of the capillary water system of the soil has already been mentioned.[1] By virtue of the surface-tension forces on the innumerable curved surfaces of this water system, the water films are able to thicken or to become thinner as water is supplied or withdrawn, and without any general distruction of the water system as a whole. In this way the capillary system serves as an important storehouse of water in soils which are below saturation. As the water films become thinner or thicker in response to changes in the amount of water, it is obvious that air will be pulled into the soil or forced out of it. Every shower thickens the capillary water system and forces air out

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[1] Pages 62 and 63 above.

of the soil. During the following dry period plants use this capillary water or it is lost by surface evaporation, the capillary water system is thinned and air is drawn into the soil. The quantitative importance of this form of soil ventilation depends upon so many factors and such complex ones that it is impossible to estimate it accurately. It is certain, however, that it is among the most important of the factors acting and it is quite probable that it is the most important one.

The circulation of gases, as a result either of water changes or of differences in temperature, is a circulation by virtue of differences of gas pressure. Physically, this is the case of movement of gases through a porous medium under a small pressure or "head", and it is important to see how largely this depends on the size of the passages in the porous medium. It is usually assumed that the flow of gas through soils is represented by the formula of Poiseuille[1] for the flow of fluids through capillary tubes. This formula is:

$$Q = K \frac{hd^4}{l}$$

in which "Q" is the rate of movement of the fluid, "h" is the "head" or driving pressure, "d" is the diameter of the passage, "l" is its length and K is a constant which depends

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[1] Ann. Chim. Phys. (3) 7: 50 (1843).

on the properties of the fluid. It is by no means certain that this formula really applies to the movement of air in soils[1] but whatever the actual expression, it will probable contain a high power of the diameter of the passage. It will be noted that the Poiseuille formula contains the fourth. This means that the rate of flow will decrease very rapidly as the passages become smaller and this conclusion is in general agreement with the results of experiments on the subject.[2] It follows that ventilation by convectional circulation or as the result of water movements will be very much more difficult in clay soils than in sands.

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[1] See, for instance, Leather,- Jour. Agr. Sci. 4: 303-304 (1912).

[2] On the flow of air through soil under external head see: Ammon,- Forsch. Geb. Agr. Physik. 3: 209 (1883); von Welitschkowsky,- Arch. Hyg. 2: 483 ( ); Hannan,- Forsch. Geb. Agr. Physik. 15: 6-25 (1891); Wollny,- Forsch. Geb. Agr. Phys. 16: 193-222 (1893); Heinrich,- Ber. landw. Vers. Stat. Rostock 2: 40-72 (1894); Deherain and Demoussy,- C. R. 122: 109-112 (1896); King,- U. S. Geol. Survey, Ann. Rep. 19, II; 59-294 (1897-1898), Wisc. Agr. Exp. Sta., Report 1898: 123-133, Science 22: 495-499 (1905); Renk,- Zeits. Biol. 15: 205 ( ); Green and Ampt,- Jour. Agr. Sci. 4: 1-24 (1911), 5: 1-26 (1912).

This relation of ease of aeration to the mean size of individual pore spaces applies, theoretically, only to ventilation by gas movement under pressure. An expression representing gas exchange by diffusion would contain the second power of the porosity,[1] but porosity refers to total relative pore space and not at all to the mean size of the individual pore spaces. On this theory the diffusional gas exchange out of a clay soil would be just as great as out of a sand; probably greater since the clay would usually have a greater total pore space. Now, as a matter of fact all of the cultural, bacteriological and chemical symptoms which are supposed to indicate bad soil aeration are much more prone to appear on heavy clay soils than on the lighter loams and sands. This may be due to a failure of the diffusion formula to remain independent of the individual pore-size when this size is

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[1] See page 26 above.

very small[1], but it is much more likely to mean that molar gas exchange resulting from water movement is relatively more important than is diffusion. Such molar gas exchange, as noted, will be greatly lessened in heavy soils because of the smallness of their individual pore spaces.

In addition to the oxygen and carbon dioxide in gaseous form in the soil both of these gases are normally present in the soil solution and the oxygen so supplied is probably quite important to the respiration

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[1] This might occur, for instance, because of the effect of adsorbed films of gas held more or less permanently on the surface of soil particles or water films. The interference of water vapor is also a possibility. On adsorbed gas films in soils see Patten and Gallagher,- U. S. Bur. of Soils, Bull. 51, 50 pp. (1908); Ehrenberg,- Bodenkolloide, pp. 223-227 (1915). On adsorption in general see Freundlich,- Kapillarchemie pp. 50-290 (1909). It is doubtful whether adsorbed gas films can have any direct action in supplying oxygen for root respiration, although this has been suggested by Ehrenberg (*loc. cit.*) and by Czapek,- Biochemie der Pflanzen, vol. 2, p. 378 (1905). If such adsorbed air is available to organisms it would soon be exhausted under anaerobic conditions. If it is not available, it is without influence.

of aerobic roots. Oxygen absorbed by rain water is carried downward as the water enters the soil and probably forms an important contribution to the soil supply. Harrison and Aiyer[1] regard this form of aeration as very important in the growing of rice on wet soils and suggest that the oxygen content of the downward-percolating water is greatly and beneficially increased by means of oxygen produced by green algae growing on the soil surface. The solubility of oxygen in water is somewhat greater than the solubility of nitrogen. Accordingly the gases absorbed by natural waters contain relatively more oxygen and less nitrogen than does the air. Water in contact with air at 20° C. and normal atmospheric pressure (760 mm.) absorbs 6.36 c.c. of oxygen and 12.32 c.c. of nitrogen per liter of water. This gives a total absorption of 18.68 c.c. of both gases, in which mixture the oxygen forms 34.03 percent (by volume)[2].

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[1] Memoirs Dept. Agr. India, Chem. Ser. 3: 65-106 (1913), 4: 1-17 (1914).

[2] Winkler,- Ber. Chem. Ges. 24: 3609 (1891). On the diffusion of oxygen in water see Carlson,- Jour. Amer. Chem. Soc. 33: 1027-1032 (1911). The carrying of oxygen into the soil by water is probably not diffusional but due entirely to mass movement of the water.

With rise of temperature the solubility of both gases decreases, that of oxygen a little more rapidly than that of nitrogen. Accordingly the percentage of oxygen in the dissolved gases is less at higher temperatures and greater at lower temperatures. For instance, at 10° C. the total dissolved gas is 22.84 c.c. per liter and 34.47 percent of this is oxygen. At 30° the total gas is 15.64 c.c per liter and the oxygen percentage is 33.60. Although all of these figures were obtained for pure water they will not be altered in important degree by any dissolved substances likely to be present in the soil solution.

The solubility of carbon dioxide in water is considerable greater than that of oxygen. At 20° C. and 760 mm. pressure of pure carbon dioxide one liter of water will dissolve 878 c.c. of the gas. There seem to be no accurate determinations of the solubility of the gas at lower pressures, approximating the partial pressure of the gas which occur in soils.[1] However, this lack is unimportant since the solubility of carbon dioxide in

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[1] There is some data on the solubility of atmospheric carbon dioxide in sea water, but the conditions are not comparable, For data see Clarke,- Data of Geochemistry, U. S. Geol. Survey, Bull. 616, pp. 143-145 (1916), and literature there cited. Carbon dioxide does not obey Henry's law of the variation of gas solubility with pressure, hence its solubility at low pres-

sures cannot be calculated. See Khanikow and Luginin,- Ann. chim. phys. (4) 11: 412 (1886).

water is affected importantly by the presence of other substances in the solution, including salts of potassium, sodium and calcium which are usually present in soil solutions. In particular, the solubility of the gas is greatly increased by the presence in the solution of alkaline carbonates or hydroxides with which the carbon dioxide can combine to form carbonates or bicarbonates. Accordingly the solubility of carbon dioxide in the soil solution will vary widely in response to differences in the chemical composition of the solution and may rise considerably above the values for pure water.[1] How much practical effect the absorption of carbon dioxide by the soil solution may have on the composition of the soil air it is impossible to say but it seems not improbable that such absorption, followed by removal in the drainage-water, may assist significantly in the removal of carbon dioxide from the soil.

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[1] Of the voluminous literature concerning the effects of dissolved substances on the solubility of carbon dioxide see: Mackenzie,- Ann. Physik (Wied.) (2) 1: 450 (1877); Geffcken,- Zeits. physik. Chemie 49: 271 (1904); Stieglitz,- Car. Inst. of Wash., Pub. 107: 235- (1909); Fox,- Trans. Faraday Soc. 5: 68-87 (1909); Johnston,- Jour. Amer. Chem. Soc. 37: 2001-2020 (1915); Johnston and Williamson,- Jour. Amer. Chem. Soc. 38: 975-983 (1916).

THE SPECIFIC PHYSIOLOGICAL EFFECTS OF CARBON DIOXIDE.

The frequent presence in the soil air of considerable percentages of carbon dioxide makes it necessary to inquire into the possibility of specific effects of this gas on plant roots in addition to the effect of its mere presence in decreasing the percentage of oxygen. We know that gaseous nitrogen is physiologically inert and has no specific effect on plants. This does not appear to be true of carbon dioxide. The effects of the carbon dioxide in the atmosphere are of little interest to the present inquiry. The process of photosynthesis is dependent on the presence of carbon dioxide and probably on its partial pressure in the air, and the rate of photosynthesis is, of course, important to the growth of a green plant as a whole, but nothing of this kind occurs in soil. The effect of increases or decreases in atmospheric carbon dioxide may be passed, therefore, with very brief notice. Slight increases in the percentage of carbon dioxide in the air have usually been found

to have favorable effects on growth.[1] Larger increases are injurious[2]. There is much conflict of evidence as to the precise percentage of carbon dioxide in the air which is most favorable to plants, this conflict being due, probably, to the fact that this optimum concentration

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[1] Godlewski,- Arb. bot. Inst. Würzburg 1: 343 (1873), 2: 495 (1880); Kreussler,- Landw. Jahrb. 14: 913 (1885), 16: 711 (1887), 17: 161 (1888), 19: 649 (1890); Jentys,- Bull. Acad. Sci. Cracovie _____: 306-310 (1892); Chapin,- Flora 91: 348-379 (1902); Demoussey,- C. R. 136: 325-328 (1903), 138: 291-293 (1904); 139: 883-885 (1904); Jardin,- 18: 221 (1904); Fischer,- Gartenflora 61: 298-307 (1912), Jahresber. Ver. Angew. Bot. 11: 1-8 (1913), Gartenflora 63: 125-132 (1914); Kisselew,- Bot. Centbl., Beih. 32: 86-96 (1914).

[2] See the articles of Godlewski and of Chapin cited ~~on page~~ in , note 1 , and de Saussure,- Recherches chimiques, pp. 25-34 (1804); Grischow,- Unters über d. Athmung, p. 33 (1819); Davy,- Elements of Agric. Chem. 3rd ed., p. 205 (1821); Boussingault,- Agronomie, vol. 4, pp. 286 ff (1868); Böhm,- Sitzungsber. Akad. Wiss., Wien, Abt. 1, 66: 18 (1872); Müller,- Bot. Unters., vol. 1, p. 353 (1876); De Vries,- Landw. Jahrb. 8: 417 (1879); Frank,- Krankheiten der Pflanzen, 2nd ed., vol. 1, p. 307 (1894); Freudenreich,- Bot. Centbl., Beih. 4: 457 (1894); Lopriore,- Jahrb. wiss. Bot. 28: 531-626

(1895); Mangin,- C. R. 122: 747 (1896), Etude sur la vegetation dans sa rapport avec l'aeration du sol, p. (1896); Brown and Escomb,- Proc. Roy. Soc. 70: 397-412 (1902); Palladin,- Pflanzenphysiol., pp. 232-233 (1911); Berkowsji,- Gartenwelt 17: 707-709, 18: 445-446 (1914).

depends on the light intensity.[1] The relation between the light intensity and the amount of carbon dioxide used in photosynthesis is obvious. The fact that considerable increases in the carbon dioxide content of the air are injurious may be due to a specific harmful effect of the gas but may depend merely on disturbances of respiration by the altered oxygen-carbon dioxide ratio of the air.[2] The various morphological modifications which frequently follow exposure to excessive percentages of carbon dioxide[3] are similarly inconclusive since these may be due merely to alterations of food supply resulting from differences in the rate of photosynthesis. That high concentrations of carbon dioxide are not necessarily fatal to protoplasm

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[1] Pantanelli,- Jahrb. wiss. Bot. 39: 167-228 (1904).

[2] However, Deherain and Maquenne report that the respiration of leaves was unaltered in air containing 40 percent of carbon dioxide,- Ann. agron 12: (1886).

[3] On such morphological changes see: Jentys,- Bull. Acad. Sci. Cracovie ______: 306-310 (1892); Teodoresco,- C. R. 127: 335-338 (1899), Rev. gen. bot. 11: 445-470 (1899); Farmer and Chandler,- Proc. Roy. Soc. 70: 413-423 (1902).

is shown by the ability of the alcohol yeast and other micro-organisms to live in the presence of large amounts of carbon dioxide,[1] rising, in the case of certain bacteria to a pressure of 50 atmospheres of the gas.[2]

More significant for the present inquiry are the disturbances of various specific vital functions which follow exposure to excessive partial pressures of carbon dioxide. Thus excess of carbon dioxide is reported to decrease the subsequent power of photosynthesis[3] and to interfere with the power of producing chlorophyll.[4]

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1. Melsens,- C. R. 70: 632 (1870); Fraenkel,- Zeits. für Hyg. 5: 332 (1889); d'Arsonval,- C. R. 112: 667 (1891); Sabrazes and Bazin,- Koch's Jahrb. _____: 34 (1894); Flügge,- Microorg., 3rd ed., vol. 1, p. 445 (1896); Jensen,- Centbl. Bakt. 6: 762 (1900); Foa,- Atti Lincei,- (5), II, 15: 53-58 (1906); Hoffman,- Arch. Hyg. 57: 379-400 (1906). As in the case of higher plants, there is much conflict of evidence concerning the minimum partial pressure of carbon dioxide which is injurious, especially to yeast. Doubtless different species or strains differ in their susceptibility.

2. Sabrazes and Bazin,- Koch's Jahrb. _____: 34 (1894).

3. Boussingault,- Agronomie,- vol. 4, p. 287 (1868); Pringsheim,- Sitzungsber. Akad. Wiss., Berlin 1887: 768; Engelmann,- Bot. Ztg. _____: 717 (1888).

4. Böhm,- Sitzungsber. Akad. Wiss., Wien _____: 14 (1873).

Jesenko[1] reports an effect of carbon dioxide in shortening the rest period of trees. According to Correns[2] excess of carbon dioxide lowers the irritability of Mimosa and Darwin[3] reports that it causes the closing of stomata. Molish[4] and Rothert[5] have observed a supposed negative tropism of roots to carbon dioxide and Engelmann[6] obtained a shock response of *Bacterium photometricum* to sudden changes in the concentration of carbon dioxide although no similar response occurred on mere replacement of the air by hydrogen. Protoplasmic streaming

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1. Ber. deut. bot. Ges. 30: 81-93 (1912).

2. Flora 75: 109, 121, 130 (1892).

3. Darwin,- Proc. Roy. Soc. 63: 413-417 (1898).

4. Sitzungsber. Akad. Wiss., Wien, 90: 172, 194 (1884), but see the contrary observations of Bennett and Sammett noted on page 5 , note 2 .

5. Flora,- Ergzbd. ________: 216 (1894).

6. Pflüg. Arch. 30: 112 (1882); Bot. Ztg. _____: 689 (1888). On chemotaxis of Paramaecium toward carbon dioxide see Jennings,- Jour. Physiol. 31 : 318 (1897).

is usually stopped by excess of carbon dioxide[1] but Josing[2] reports that streaming can continue in the presence of carbon dioxide if the cell is illuminated. Several investigators have observed a detrimental effect of excess of carbon dioxide on germination and a tendency for it to produce or lengthen the dormancy of seeds.[3] Similarly, Lopriore[4] has observed interference with the development

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1. Kühne,- Unters. über das Protoplasma p. 164 (1864); Demoor,- Arch. Biol. *13*: 190 (1893); Loproire,- Jahrb. wiss. Bot. *28*: 531-626 (1895); Klemm,- Jahrb. wiss. Bot. *28*: 636 (1895); Samassa,- Verh. naturh. Ver. Heidelberg *6*:   (1898); Ewart,- Protoplasmic streaming, p. 78 (1903).

2. Jahrb. wiss. Bot. *36*: 197 (1901).

3. See especially Kidd,- Proc. Roy. Soc., (B) *87*: 408-421, 609-625 (1914); also: Bernard,- Lecon sur les effets des substances toxiques, p. 200 (1883); Mangin,- C. R. *122*: 747-749 (1896); Marcacci,- Arch. ital. Biol. *19*: 140 (1892). Kidd reports, however, that low partial pressures of carbon dioxide may stimulate germination (*loc. cit.*, pp. 609-625). This is perhaps a case of the apparently general rule that low concentrations of poisonous substances are stimulating, see Free and Trelease,- Johns Hopkins Univ. Circ. ______: (1917).

4. Jahrb. wiss. Bot. *28*: 531-626 (1895).

of spores of mucor and of some pollen grains. Crocker,[1] however, states that some seeds cannot be rendered dormant by carbon dioxide. The experimental result of Babcock[2] that seeds die more quickly when stored in carbon dioxide than in air, may be simply a result of cessation of respiration because of the absence of oxygen. Among specific effects of carbon dioxide in the animal organism there may be mentioned its reported action in stimulating the respiratory center[3] and its probable influence on the tonus of the intestine.[4]

The evidence concerning the action of carbon dioxide on roots is even more inconsistent than that with regard to its effects on the aerial portions. Thus Jentys[5] and Chapin[6] have obtained injuries to roots by carbon dioxide and Kossowitsch[7] observed wilting of pea

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[1] Amer. Jour. Bot. 3: 115 (1916).

[2] Wisc. Agr. Exp. Sta., Res. Bull. 22, p. 98-101 (1912).

[3] Laqueur and Verzan,- Pflüg. Arch. 143: 395-427 (1912).

[4] Rona,- Zentbl. Physiol. 26: 733-734 (1912).

[5] Bull. Acad. Sci. Cracovie _____: 306-310 (1892); Bot. Centbl. 52: 93 (1892).

[6] Flora 91: 348-379 (1902).

[7] Bot. Ztg. ______: 702 (1892).

plants when the soil air contained 80 percent carbon dioxide and 20 percent air. Similarly in the experiments of Kosaroff[1], later described in detail[2], carbon dioxide caused a greater interference with water-absorption by roots than was caused by simple deprivation from oxygen. This was true both in soil and in water-cultures. Similar injuries by passing carbon dioxide through the culture solution of water-culture have been observed by Wolf[3] and by Free[4]. Birner and Lucanus[5], however, observed an increased growth on passing carbon dioxide through the culture solution.

In soil cultures, Noyes[6] has found wilting and bad growth of corn and tomato plants when the soil was saturated with carbon dioxide. On the other hand a number of investigators have obtained increased yields of various crops by blowing carbon dioxide through the

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[1] Diss., Leipzig, pp. 47-62 (1897); Bot. Centbl. 83: 138-144 (1900).

[2] See page [illegible].

[3] Jahresber. Agriculturchem. 1870-1872: 134.

[4] Johns Hopkins Univ., Circ. ________: (1917).

[5] Landw. Vers. Stat. 8: 128-177 (1866).

[6] Science 40: 792 (1914).

soil[1]. Mitscherlich[2], however, secured no increase of yield by irrigation with water saturated with carbon dioxide. It is possible, as suggested by Hansen[3], that the benefit derived from forcing carbon dioxide through the soil is really due to a slight enrichment of the air immediately above by means of the escaping gas, this enrichment being beneficial to the aerial parts of the plants. The experiments of Cannon, later described in detail[4], and one experiment included in the present investigation[5] indicate specific effects of carbon dioxide on roots[6] but the tests are not numerous enough to permit clear dissociation from the effects of the mere

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[1] Demoussy,- C. R. 138: 291-293 (1904); Wagner,- Mitth. deut. landw. Ges. 25: 176-179 (1910); Hansen,- Naturw. Rundschau 27: 547-550 (1912); Hiltner,- Prakt. Bl. Pflanzenbau and Schutz (n.s.) 11: 45-52 (1913); Bornemann,- Mitth. deut. landw. Ges. 28: 443-445 (1913); Quarrie,- Commercial Fert. 8: 26c (1914); Reinau and Klain,- Gartenwelt 18: 214-218 (1914).

[2] Landw. Jahrb. 39: 157-166 (1910).

[3] Naturw. Rundschau 27: 547-550 (1912).

[4] See pages 91-94.

[5] Page 127.

[6] See especially Car. Inst. of Wash., Yearbook 15: 74-75 (1916) and Cannon and Free,- Science 45: 178 (1917).

removal of oxygen. No direct evidence supports Mitscherlich's[1] opinion that the carbon dioxide in the soil is beneficial and that a degree of aeration sufficient to remove this gas is detrimental.

The conflicting nature of the evidence makes impossible any final decision concerning the effect of the carbon dioxide of the soil air on the roots or other portions of plants. It is probable, however, that the nature of plant and of soil affect the reaction and that a concentration of carbon dioxide toxic to one plant in a given soil might not be toxic to other plants, or to the same plant in another soil. Similarly in water-cultures the plant grown and the composition of the solution may affect the result. Whether the effect of carbon dioxide on roots resembles its effect on shoots in that there is a stimulation by small concentrations cannot be determined from existing data. The experimental cases of benefit from application of carbon dioxide to the soil may be explained by secondary reactions, such as effects on micro-organisms[2] or the well-known effect of dissolved

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[1] Bodenkunde, 2nd ed., p. 248 (1913).

[2] For instance, the stimulation of the nitrifying bacteria by carbon dioxide. See Owen,- Georgia Agr. Exp. Sta., Bull. 87 (1907).

carbon dioxide in increasing the solubility of minerals in the soil solution and thus assisting the nutrition of the plant.[1]

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[1] On the effect of carbon dioxide in increasing the solubility of minerals see Sachsse,- Lehrb. Agriculturchem. p. 181 (1888); Cameron and Bell,- U. S. Bur. of Soils, Bull. 30, pp. 32-34 (1905); Engels,- Landw. Vers. Stat. 77: 269-304 (1912); Mettler,- Zeits. Sauerstoff und Stickstoff Indust 5: 193 (1913); Mitscherlich,- Bodenkunde, 2nd ed., pp. 153, 178-187 (1913); Clarke,- Data of Geochem., U. S. Geol. Survey, Bull. 616: pp. 478-486 (1916). Further literature is cited by these authors, especially Cameron and Bell, and Clarke. On the solvent action of roots and of bacteria due to excreted carbon dioxide, see: Sachs,- Bot. Ztg. ______: 117 (1860) (This is the original observation of root-prints on a marble slab, then interpreted as due to organic acids); Kossovich,- Zhur. Opyt. Agron. 5: 482-493 (1904); Hall,- Science Prog. 1: 51-57 (1906); Bassalik,- Zeits. für Gärungsphysiol. 2: 1-32 (1912); Pfeiffer and Blanck,- Landw. Vers. Stat. 77: 217-268 (1912); and the authorities on excretion of carbon dioxide by roots cited on page 5, note 1. On the action of carbon dioxide in modifying soil flocculation through changes in the solubility of the salts of magnesium and calcium see: Ehrenberg,- Bodenkolloide, pp. 432-434 (1915).

PREVIOUS EXPERIMENTS ON THE OXYGEN REQUIREMENT OF PLANT ROOTS.

There have been mentioned above two series of investigations which throw, indirectly, some light on the need of roots for oxygen though neither line of experimentation is conclusive or satisfactory. First are the observations on the rate of respiration of various roots.[1] It has already been indicated that these are of little significance for the reason that the observed occurrence of normal aerobic respiration in the presence of oxygen does not prove that the same tissue could not respire anaerobically if oxygen were withheld. Second are the experiments of Jentys, Chapin, Noyes, and others in which the normal soil atmosphere was replaced by carbon dioxide, resulting in more or less serious injuries to the plants.[2] One result of such replacement is to deprive the roots of oxygen but it is by no means certain that this deprivation is the sole cause of the observed injury or that it is a cause of injury at all. Not only do the probable specific effects of carbon dioxide come into play but the possible presence of traces of oxygen, possible variations of water supply, individual plant variation, and the like were not taken

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1. Page 7 .
2. Pages 52-54

sufficiently into account to give the experiments important weight for an inquiry into the oxygen requirement of plant roots. These experiments need not be considered further. There are, however, two previous investigations which must be reviewed in a little more detail. These are the work of Kosaroff and that of Cannon, both of which have been mentioned already.

The experiments of Kosaroff[1] were incidental to an investigation of the effects of various factors on water absorption by plant roots. Experiments were made in soil with *Phaseolus multiflorus* and *Vicia faba* and in water culture with Phaseolus only. For the soil experiments the ordinary clay pot containing the plant was placed in a somewhat larger glass jar and this jar was covered with a split glass cover, the stem of the plant projecting through a hole in the center of the glass cover so that the aerial portion of the plant projected into the atmosphere. The glass top was then sealed to the glass jar with grafting wax and a similar seal was made between the glass top and the stem of the plant. The soil, containing the plant roots, was thus enclosed in an air-tight space. The desired gas was now passed through this by means of tubulatures in the glass

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[1] Einfluss verschiedener äusseren Factoren auf die Wasseraufnahme der Pflanzen, Diss., Leipzig, 64 pp. (1897); Bot. Centbl. 83: 138-144 (1900).

jar and the glass top. Phaseolus was tested with pure carbon dioxide, with 90 percent carbon dioxide and 10 percent air, with 80 percent carbon dioxide and 20 percent air, and with hydrogen. With the pure carbon dioxide the plants wilted in from ¼ to 1 hour. With 90 per carbon dioxide the wilting occurred in from 1 to 2 hours, and with 80 percent carbon dioxide, in from 2 to 3 hours. After wilting by exposure to pure carbon dioxide the plants revived if air was passed through for from 1 to 1½ hours. Use of hydrogen instead of carbon dioxide produced no effect. The total time for which the hydrogen was passed is not stated. Experiments with Vicia and pure carbon dioxide gave substantially the same result except that the wilting occurred only after 3 to 4 hours. Hydrogen was again without effect. It is obvious that these experiments, except for the trial of hydrogen, go little beyond the earlier results of Jentys. The negative result with hydrogen also has little significance for the reason that the time of the experiment, although not stated, was probably too short to disclose any effect of root suffocation had one been possible. Hydrogen, in itself, probably has no effect, its only action being to replace the oxygen.

The experiments in water-culture were made quantitatively, the effect on the rate of water absorption by the roots being measured by determining the transpiration from the culture under the various treat-

ments. Transpiration was determined by weighing the entire culture at the beginning and end of the observation period.[1] The method was to run air through the culture solution for from 20 to 60 minutes, then to run through a stream of the gas under test for a like period. The difference in the transpiration indicated the effect of the gas. Experiments by this method with pure carbon dioxide gave decreases of transpiration of approximately 50 percent. Mixtures of 90 and 80 percent carbon dioxide with air gave somewhat smaller decreases of transpiration. Hydrogen also decreases the transpiration but to a less extent than did carbon dioxide. The average decrease was about 25 percent. When carbon dioxide was followed by air the transpiration rate went up again almost to its initial value. When carbon dioxide was followed by hydrogen the transpiration rate rose to about the same value as when hydrogen was used following air. Experiments on plants the roots of which had been killed by dipping in boiling water showed a decrease of transpiration rate with carbon dioxide but none with hydrogen. Experiments with cut twigs of _Tilia pubescens_, _Sparmania africana_ and _Abutilon striatum_

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[1] It is obvious that this does not measure root absorption if there was loss or gain of water by the plant tissue, as, for instance, by wilting. However, the error is probably without effect on the general meaning of the results.

showed decreases with both carbon dioxide and hydrogen much like those observed with living plants of Phaseolus but slightly less in amount.

From the present viewpoint the significant things in these experiments are, first, the injury by hydrogen and, second, the fact that injury consisted in an interference with water absorption. The importance of this second conclusion will be apparent when the experimental results of the present investigation are presented. The action of hydrogen implies a need of the roots of Phaseolus for oxygen but the evidence leaves much to be desired in precision and finality especially since it was obatined in water-culture and since the other evidence concerning the effect of aeration in water cultures is so seriously contradictory.[1] The evidence of the detrimental effect of carbon dioxide both in soil and in water-culture appears to be conclusive but means nothing for the problem of the oxygen requirement of the roots.

The experiments of Cannon[2] have been made incidentally to an investigation of the distribution

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[1] See pages 50-51

[2] Car. Inst. of Wash., Yearbook 11: 62 (1912), 14: 62-64 (1915), 15: 74-75 (1916); Amer. Jour. Bot. 2: 211-224 (1915); Amer. Nat. 50: 435-442 (1916); Science, 44: 761 (1916). See also Cannon and Free, Science 45: 178-180 (1917).

of plant roots in the soil with relation especially to temperature and aeration. Dr. Cannon's data have not yet been published in detail and I am indebted to him for fuller memoranda of his results than have appeared in the preliminary notices which have been published. His technique differs essentially from any heretofore employed in this field. A small plant of the species to be examined is grown in sand in a glass tube 2 cm. in diameter and 30 cm. long. This tube can be sealed at the top, around the plant, with modeling clay or other plastic and side tubes at the top and bottom permit the control of the atmosphere inside the culture tube. Water can be supplied when necessary through a perforation in the seal at the top and can be allowed to drain off at the bottom. Under these conditions some one or more of the plant roots will lie close to the glass tube and can be observed through it. The method consists in observing the rate of elongation of such an individual root over short periods when the atmosphere in the tube is of known character. Observations are made by a horizontal microscope or by an automatic device which photographs the position of the root tip at regular time-intervals. The rate of elongation is first measured in air, then the gas under examination is allowed to flow through the tube and the rate of elongation is measured again. The temperature must be kept constant.

Using this method experiments have been made with roots of *Opuntia versicolor* (cactus) and of *Prosopis velutina* (mesquite) in air, in carbon dioxide and in various mixtures of carbon dioxide with air and with oxygen. It was found that the roots of Opuntia are much more sensitive to carbon dioxide than are those of Prosopis. A mixture of 50 percent carbon dioxide with 50 percent oxygen stopped the growth of Opuntia roots while those of Prosopis were unaffected in growth rate by concentrations of carbon dioxide as high as 75 percent. An atmosphere of 90 percent carbon dioxide and 10 percent air (containing, therefore, only 2 percent oxygen) slowed the growth rate of Prosopis roots but did not stop it entirely. However, both Prosopis and Opuntia ceased to grow in pure carbon dioxide. Aeration by drawing air through the tube increased the growth rate of Opuntia but had little effect on that of Prosopis. Collateral experiments by other methods have shown that the development of the root system of Opuntia is favored by good soil aeration while Prosopis is relatively little effected. The roots of the ocotilla (*Fouquieria splendens*) are also stimulated by good aeration.

The most significant thing in these experiments is the sharp difference discovered between the responses of Opuntia and Prosopis. This strongly reinforces the inference from other literature that different plants

may differ widely in their response to oxygen deficiency in the soil or to the presence of excess of carbon dioxide. From this fact Cannon makes certain ecological deductions to which it will be necessary to refer below. Another significant result in Cannon's work is the fact that root growth of Prosopis stops in pure carbon dioxide and is slowed in the mixture with 10 percent of air although a specific effect of carbon dioxide is improbable since growth continued normally in mixtures containing 75 percent of this gas. Apparently the stoppage of growth in the higher concentrations of carbon dioxide must be ascribed to deficiency of oxygen rather than to excess of carbon dioxide and, except for the experiments of the present investigation this is the first piece of real evidence that plant roots are injured by anaerobic conditions. It appears that Opuntia is injured specifically by excess of carbon dioxide since growth stopped in a mixture of 50 percent carbon dioxide and 50 percent oxygen. Probably Opuntia roots are as sensitive to deficiency of oxygen as are those of Prosopis but this cannot be determined from the data since the specific effect of the carbon dioxide intervenes.

The experiments which will be described in the following chapters have been noted in several ad-

vance notes and abstracts of results[1], all data of which will be repeated in the following pages.

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[1] Free and Livingston,- Car. Inst. of Wash., Yearbook 14: 60-61 (1915); Livingston and Free,- Car. Inst. of Wash., Yearbook 15: 78 (1916), Johns Hopkins Univ., Circ. _______: (1917); Cannon and Free,- Science 45: 178-180 (1917).

EXPERIMENTAL METHOD.

The method employed in the experiments here reported is a modification of the methods already used by Jentys, Kossowich, Kosaroff and Noyes in their studies of the effects of carbon dioxide and other gases on plant roots. It will be remembered, as described above for the experiments of Kosaroff, that this technique consists in sealing the roots (with the soil in which they lie) into a container through which the desired gas can be passed. The stem of the plant projects through the seal so that the aerial portions are exposed to the general atmosphere. In the experiments of the investigators mentioned the duration of a single experiment was never more than a few hours and for such short times the technique offers no important difficulty. However, as noted in describing the results of Kosaroff with hydrogen, such short-time experiments are not adequate for the investigation of the nature of root respiration. It is probable that almost any plant can endure anaerobic conditions for a short time. If real anaerobic respiration of roots is to be realized experimentally by this method, it must be possible to grow plants for long periods with their roots in soil which is sealed-off from the general atmosphere so that the composition of its own internal atmosphere may be controlled. This necessity for experiments of longer

duration introduces several experimental difficulties not met with in the shorter experiments of previous investigators and which difficulties it has been necessary to overcome. The three most important of these difficulties are the maintenance of a permanent seal about the plant stem, the supply of water without breaking the seal, and the control of the soil atmosphere without consuming an impossibly large quantity of the needed gases. A seal which is sufficiently permanent has been devised and will be described in detail. The difficulty of water supply has been met by the use of the porous cup auto-irrigator as devised by Livingston.[1] In the experiments of Kosaroff and other previous investigators the control of the composition of the soil atmosphere was secured by passing through the pot containing the sealed-in soil a stream of gas having the desired composition. This method is impracticable in experiments running over weeks or months because of the large quantities of gas which would be required, the cost of this being prohibitive for all gases except air. There has been devised, therefore, a static method of controlling the soil atmosphere which will be described in detail and which does not require the passage of a stream of gas. By this method the consumption

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[1] Livingston,- Plant World 11: 39-40 (1908); Hawkins,- Plant World 13: 220-227 (1910); Livingston and Hawkins,- Car. Inst. of Wash., Pub. No. 204: 5-48 (1915).

of the gaseous reagents is inconsiderable.

The general arrangement of the apparatus may be described as follows. The plants are grown in cylindrical tin cans 7 inches (18 cm.) deep and 6 inches (15 cm.) in diameter. These are standard "soldered" cans which can be obtained from the American Can Co. at small cost. All joints are soldered. In the can with the plant are the three porous cups of the auto-irrigator system. Glass tubes, connected with the two end cups project above the soil and suffice for water supply to the cups and for cleaning, as described below. Into the top of the tin can, about one half centimeter (.2 inch) above the soil there is soldered a tin top perforated with three holes; one, centrally placed, for the plant stem, and two, toward the periphery, for the connecting tubes of the auto-irrigator. If necessary the top is split to permit easy insertion of the plant stem through the central hole. This tin top is intended merely to provide mechanical support for the seal about the stem of the plant, which support is necessary if the seal is to withstand the shocks and bendings of the stem incident to wind-movement of the plant, to taking ahold of the can in moving it, and the like. No attempt is made to solder the tin-top perfectly to the can or to secure an hermetical seal at the soldered joint. The real seal at this joint and about the projecting connection tubes for the auto-irrogator is secured by

ordinary sealing wax, applied hot and sealed down to the tin and glass surfaces by subsequent careful application of the flame of a gas-blowpipe. Connections with the outside, for purposes of control of the soil atmosphere, are provided by two tubes; one of glass, inserted by the side of the water-tube through one of the holes in the top; the other of lead, soldered into the side of the tin can toward the bottom. The glass tube at the top is sealed in with sealing-wax in the same way as is the water-supply tube. The soldered joint between the lead tube and the side of the tin can is made air-tight. The general arrangement of the can, plant, and connection tube is shown in figure 1.

The seal around the plant stem presented considerable difficulty. The simple seal of wax or grafting-wax, as used by previous investigators, will not last more than a few days without cracking and allowing leakage. It is necessary that the seal remain air-tight and yet permit the slow enlargement of the stem which accompanies the growth of the plant. It is obvious, also, that the seal must not require contact of the stem with any substance which will be injurious to it. Many devices were tried and discarded. Split rubber stoppers, or rubber tissue wrapped about the stem were found to be unsatisfactory because of interference with enlargement of the stem and consequent

injury to the plant. Solutions of rubber in gasoline and other solvents, and similar "rubber-cements" were found, as was expected, to be injurious to the tissue of the stem. Glue, gelatine and similar hydrophillous colloids were found to draw water from the stem and become soft and liquid, permitting easy blowing-out of the seal. Parafine, and various parafine-vaseline mixtures, as, for instance, the mixture of Briggs and Shantz,[1] would not maintain permanent contact with the stem but would crack away from it, allowing gas leakage through the space thus formed. The problem was solved by means of a seal of grafting-wax applied as shown in section in figure 2. A collar of sealing-wax is first built up around the stem for about 1 centimeter (.4 inch) above the tin top. This collar is in the form of a cylinder resting on the tin top and with its inner surface about 3 to 4 millimeters from the plant stem. Its actual diameter, as well as the diameter of the hole below it in the supporting tin top, will depend on the diameter of the stem of the plant which is being sealed. The sealing-wax of this collar is applied in very viscous condition and great care must be taken not to allow it to flow inward and touch or burn the stem. After it is applied its outer edge must be sealed down to the

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[1] Bot. Gaz. 51: 210-219 (1911).

tin top, or to the sealing-wax applied on top of the tin, by careful application of a very small flame of the gas blowpipe. The sealing-wax collar is indicated at "a" in figure 2.

Into the lower part of the annular space between the stem and this sealing-wax collar cotton is stuffed, as indicated at "b" in figure 2. This cotton extends outward, under the tin top, a centimeter or more from the lower edge of the sealing-wax collar. The sealing-wax collar and the cotton plug having been prepared as shown melted grafting-was is poured into the annular space around the stem. This grafting-wax saturates the cotton and fills the annular space above it, as indicated by "c" in figure 2. The grafting-wax must be at a temperature at which it is a very viscous liquid. If it is too hot it will flow through the cotton and escape. If it is too cold it will fail to saturate the cotton or to fill all the interstices of the annular space and will not bind tightly to the stem and to the inner surface of the sealing-wax collar. It is also necessary, of course, that the grafting-wax be not so hot as to burn the plant stem. For the ordinary variety of grafting-wax the proper temperature is about 65° C. (150° F.).

In this seal, the long plug of grafting-wax inside the sealing-wax collar does not harden or crack as rapidly as if applied alone, without the sealing-wax

collar. It is also firmer mechanically and resists the tendency to be blown out by slight internal pressures in the can. This tendency to resist blow-out is increased, also, by the cotton plug in the lower part of the sealing-wax collar. At the same time the grafting-wax plug remains sufficiently plastic to permit expansion of the stem by growth. The important considerations in making the seal are, first, to have the annular space between the stem and the sealing-wax collar long enough and not too wide, and, second, to apply the grafting-wax at the proper viscosity, which means the proper temperature. The necessity of this proper temperature has already been explained. If the annular space for the grafting-wax plug is too short or too wide the seal will blow out. Under most conditions the dimensions given above will be fully satisfactory. It is also necessary, of course, to use great care not to burn the plant when soldering-in the top or sealing-down the collar and various seals of sealing wax. The flame of the gas-blowpipe should be made very short (not over 2 cm.) and handled carefully. If desired, the plant can be protected by an inverted cone of asbestos paper wrapped about it and supported from above by a ring-stand and clamp, but this precaution is unnecessary with sufficient care and skill in handling the gas-blowpipe. In making the soldered joints no acid or other flux should

be used, because of danger of escape of metallic compounds into the soil. With clean tinned surfaces, there is no difficulty in making the soldered joints without flux using wire-solder and the gas-blowpipe. A soldering-iron is much more difficult to handle and less satisfactory. The sealing-wax should be of the best quality. The red variety, as furnished by Dennison and on sale at all stationery stores, was found quite satisfactory. It should be melted gently in a dish and must not be burnt or overheated prior to application.

Seals made in the manner described have been applied to nearly one hundred plant individuals of eight species with only one case of injury, this case being due, probably, to an undetected injury with the gas-blowpipe during sealing. Seals have lasted as long as 4 months without leakage, but in some cases cracking and leakage will occur in 4 to 6 weeks, especially if the enlargement of the stem is rapid. This cracking may be repaired by cautious softening of the grafting-wax with a stream of hot air or with a very small flame of the gas-blowpipe; or, more safely, by pouring new grafting-wax (melted as before) into the cracks and building it up (when semi-solid) further about the stem. In cases of extremely rapid growth the stem may enlarge so much as to reach and press upon the inner surface of the sealing-wax collar. In this case the old collar must be cracked away and a new and larger one built up and filled

with grafting-wax as before. If it is desired to maintain the soil atmosphere unchanged during this operation a slow stream of the proper gas can be kept flowing through the pot and outward past the stem while the seal is being reconstructed.

In very hot weather the grafting-wax may become so soft that it leaks downward by gravity or blows out under slight internal pressure. This can be prevented by using a grafting-wax of higher melting point (that is, one containing more rosin), by making narrower the annular space between the sealing-wax collar and the stem, or by packing cotton, later saturated with melted grafting-wax, very tightly into the lower third of the annular space between collar and stem. None of these expedients is fully satisfactory and it is better not to attempt experiments in very hot weather. The unmodified technique has been used successfully with greenhouse temperatures up to 35° C. (95° F.). At such high temperatures it is well to shade the seal from the sun by means of a paper collar, a covering tuft of cotton, or some similar device.

The three porous clay cups of the auto-irrigator system are arranged in the soil at the apices of a triangle at the center of which is the plant. The connections between the cups and to the water reservoir are shown in figure 3, the three cups being here shown in line, instead of in the triangular arrangement

actually employed. All connections are by glass tubes. The U-tube "a" contains a column of mercury the function of which will be described below. The tube "v" communicates with a vacuum line by means of which the cups can be drawn full of water or washed out, when necessary. When not in use this tube is closed by a pinchcock on the rubber tube connecting it with the vacuum line, as described below. The enlargement in the U-tube above the mercury column is for the purpose of preventing the accidental drawing of the mercury into the cups when water is being drawn through under vacuum. The nearly horizontal arm above and to the right of the enlarged portion is slightly inclined upward toward the right for the same reason. The dimensions given in figure 3 have been found satisfactory but are not essential. Water taken is measured by means of the scale on the water-reservoir "b", which reservoir is refilled through the tube at the left. A number of pots can be arranged conveniently as shown in figure 4, the connections from the vacuum end of the porous cup system and from the water-supply tube of the water reservoir, being brought by rubber tubes to main vacuum and water lines which lie on the board in front of the pots. Both connections are closed by pinch-cocks on the rubber tubes. The U-tubes containing the mercury columns pass under this board and connect the water reservoirs in front with the pots behind.

The theory of the auto-irrigator has been described in the papers of Livingston and of Hawkins cited above. In brief, it is as follows. It will be remembered that water is held in moist but unsaturated soils in the from of a system of water-films in the capillary spaces between the soil grains.[1] Because of surface tension on the curved surfaces of these films the water in this film system is always under a hydrostatic tension. The individual films tend to thicken and the film-system as a whole tends to draw more water into the soil. It is this capillary tension which draws water upward into a soil against gravity. The actual amount of the tension depends on the nature of the soil, being greater in soils composed of finer particles; and also on the wetness of the soil, being greater when the soil is relatively dry which means that the films are thinner and more curved. Accordingly water is drawn by capillarity from wetter portions of a soil to dryer portions, or, between two soils, from the soil of coarser particles to that of finer; always provided, of course, that the capillary film-system is in contact throughout. When the porous clay cup of the auto-irrigator is placed in a soil the water in the cup penetrates the porous clay of the cup and establishes

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[1] See pages 62,63,68), above.

contact with the capillary film-system of the soil. The tension of the latter then draws water from the auto-irrigator and will draw it against a considerable opposing tension, as, for instance when the water reservoir is placed at a lower level and water must be drawn against a gravity head due to this difference in levels. Another method of providing an opposing tension is to insert a mercury column, as was done in the connecting U-tube used in these experiments and described above. Water is then drawn against a head equal, with allowance for differing densities, to the heighth of the column of mercury.

The amount of this opposing head furnished by water or mercury columns, regulates the amount of water in the soil. It was noted that the capillary tension of the water-film system in the soil decreases as the soil becomes wetter. If, therefore, an auto-irrigator cup be placed in a relatively dry soil and allowed to establish connection with the capillary film-system, water will be drawn by the soil from the cup until the soil becomes wet enough for its capillary tension just to balance the opposing tension, or head, of the water in the auto-irrigator. In these experiments the water content of the soil in the pots was kept nearly constant automatically in this way. As water was taken from the soil by the plant roots, more water was drawn by the soil from the auto-irrigator. The actual water conten

thus maintained in a given soil depended on the nature of the soil, the temperature (as described below), and the heighth of the mercury column, but not at all on the rate or amount of water intake by the plant. When necessary the water content of the soil could be varied by removing or adding mercury and thus changing the heighth of the column.

It will be noted that, over considerable time periods, the water intake by the plant must be balanced by the water lost from the auto-irrigator. This loss may be measured on the scale of the water-reservoir. A means is thus available for measuring the water intake by the plant, but one disturbing factor must be taken into account. It was noted above that the capillary tension on the water-film system in the soil is due to surface tension. The amount of the capillary tension depends, therefore, on the intensity of this surface tension (per unit of surface) as well as on the nature of the soil and its wetness. The specific surface tension of water varies with two factors which may come into play in the case under examination; the temperature and the presence of dissolved substances. The presence of dissolved substances is probably not important practically since the substances so present in the soil solution of any particular soil are presumably constant and of constant effect on surface tension. Hence they do not affect the precision of the balance between

intake of water by the plant and loss of water from the reservoir. The effect of temperature is more important. The change in the surface tension of water with temperature is shown in the following table.[1]

SURFACE TENSION OF WATER.

Temperature (degrees C.)	Surface Tension (~~dryness~~ dynes per centimeter)
0	73.21
10	71.94
20	70.60
30	69.10
40	67.50
50	65.98
80	60.84
100	57.15

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[1] Data are from Ramsey and Shields, by capillary rise, Zeits. phys. Chem. **12**: 433 (1893). For other data, including data by other methods, see Landolt and Börnstein, Physik,- Chem. Tab., 3rd ed., p. 113 (1912) and Morgan and McAfee,- Jour. Amer. Chem. Soc. **33**: 1275-1290 (1911). For equations of relation of surface tension to temperature see Landolt and Börnstein, *loc. cit.*, p. 131, and Morgan and McAfee, *loc. cit.*, p. 1283. A good general discussion of surface tension will be found in Freundlich,- Kapillarchemie, pp. 3-89 (1909).

It is apparent that rise of temperature is accompanied by a decrease of the surfacc tension. The same rule applies to all pure liquids and to most solutions which are likely to be present in soil.[1] Accordingly, with all other conditions the same, the capillary tension on the water-film system of a soil will be less at higher temperatures and greater at lower temperatures. Correspondingly, the water-film system will hold, against a given exterior tension, more water when the temperature is low than when it is high. Under the conditions of these experiments this means that when the temperature is falling the water loss from the reservoir is slightly more than the water intake by the plant, the difference going into storage in the water-film system of the soil. That is, with falling temperature this water-film system increases somewhat in water-holding capacity. Conversely, when the temperature is rising, the water loss from the reservoir is slightly less than the water

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[1] On the surface tension of solutions see Freundlich,- Kapillarchemie, pp. 49-81 (1909) and data given by Landolt and Börnstein,- loc. cit. pp. 128-129. The occurrence of solutions the surface tension of which rises with rising temperature, instead of falling as in pure liquids, is due to the varying adsorption of the dissolved substances at the surface. See Freundlich, loc. cit.

intake by the plant, the balance being water freed from the water-film system because of its lowered capillary tension. The practical effect of this is that readings of the water loss from the reservoir do not represent precisely the actual water intake of the plant if the temperature has changed between the initial and final reading. If the temperature has fallen, as, for instance, in the evening, the reading will be too high. If it has risen, as in the morning, the reading will be too low. If should be noted that the error occurs only in the case of *change* of temperature. If the temperature is constant, the reading of water loss represents accurately the water intake by the plant, regardless of what the temperature actually is.. Similarly, there is no error if the temperature of the initial and final readings be the same, regardless of how the temperature has varied in the meantime.[1] Thus a twenty-four hour period usually has about the same initial and final temperatures, especially if the readings are made relatively early in the morning or relatively late in the afternoon. Accordingly a reading of water-loss over such a twenty-four hour period is not likely to vary widely from the actual intake of water by the plant. Slow seasonal changes of

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[1] f course, the changes must be slow enough to permit constant maintenance of equilibrium.

temperature are distributed over so many successive daily periods that their effects on the accuracy of this relation between reservoir-loss and plant-intake are negligable. There are, of course, progressive changes in water content of the soil as the season changes from cold to warm, or vice versa, but these do not affect the accuracy of the daily relation between loss and intake. In the experiments here reported it was assumed that the twenty-four-hour water-loss from the reservoir was equal to the intake by the plant over the same period. It is possible to test the reaction of a particular pot and soil to varying temperature and thus to obtain and apply a correction, but this is an extreme of accuracy which is not justified by the other conditions of the experiments. The reasons for this will be obvious when the experiments are described .

In most cases no precautions were taken to remove oxygen from the water supplied through the auto-irrigators. However, in those experiments in which it was important to come as close as possible to excluding all traces of oxygen, the water-reservoir of the auto-irrigators were provided with water from which the free oxygen had been removed by boiling. In this case, the boiled water was kept in a reservoir provided with an atmosphere of nitrogen, and the water-reservoir of each individual auto-irrogator was also provided with a nitrogen atmosphere. Usual devices were employed

for maintaining this closed nitrogen atmosphere in contact with the water supply, and for compensating its changes of temperature and pressure.

It has already been explained that the customary method of controlling the soil atmosphere by passing a stream of the desired gas was impossible because of the very large gas consumption which it would have required. On the other hand, simply to replace the normal soil atmosphere with the desired gas and then seal the pot as, for instance, by closing the inlet and outlet tubes, is impracticable because of the considerable variations of the gas pressure inside the pot which accompany changes of temperature. If such a tightly sealed pot be warmed, as at midday, the gas pressure inside becomes sufficient to blow out the seal or cause important leakage through it. On the return of lower temperatures, as at night, the pressure inside the pot becomes lower than that of the general atmosphere and leakage occurs inward. It is obvious that the repetition of this process will pump atmospheric air in and out of the pot and will destroy the value of the experiment. Theoretically there might be constructed a seal capable of withstanding this ~~diernal~~ diurnal pressure change but practically it was found impossible to do so, at least with any simple modification of the sealing technique described above. It is necessaty, therefore, to have some means by which expansion and contraction of the soil gases may be per-

mitted without allowing contact with the general atmosphere. This means is found, conveniently, in a thin rubber gas bag attached to one of the gas outlet tubes of the pot, as shown in figure 5. It is convenient to use for these gas bags the rubber bladders made for basket balls or, if desired, a still larger bladder of the same form which can be obtained from the rubber trade. The walls of the gas bag must be of light weight and very elastic. If such a bag is filled only about half full, it will expand as the temperature rises and contract~~s~~ as it falls, keeping the pressure in the pot nearly constant. As long as there is any gas in the gas bag there will be a slight positive pressure in the pot, due to the elastic tension of the rubber. This pressure must not be high enough to blow out the seal, hence the requirement that the walls of the gas bag be thin. This slight internal pressure provides that the minor leakage which it is nearly impossible to prevent, will be outward and without effect on the experiment. The plumpness of the gas bag is a convenient index that the seal is holding satisfactorily, any leakage being indicated immediately by the flattening of the bag.

In beginning an experiment a stream of the desired gas is run through the pot until the normal soil atmosphere is believed to be displaced. This may be done conveniently by attaching successively to one outlet of the pot several gas bags filled with the desired gas and allowing the gas to escape through the pot,

leaving by the other outlet tube. When the replacement of the original atmosphere is considered sufficiently complete, a gas bag half filled with the desired gas is attached to one outlet tube and allowed to remain, the other outlet tube being closed by a cork or by a pinch cock on a rubber tube. If it be desired to change or renew the artificial soil atmosphere, as, for instance, for the purpose of removing carbon dioxide or other gaseous excreta from the roots, this process of passing gas through the pot and attaching a bag full of fresh gas may be repeated as often as desired. The use of rubber tubes and pinch cocks on the outlet tubes of the pots makes it possible to accomplish such changes or renewals without danger of leakage from , or to, the general atmosphere.

There is a theoretical possibility of error in this method owing to the ability of most gases to diffuse through rubber membranes. This seems, however, to be too slight to be important in the present experiments. A gas bag half filled with nitrogen, closed and exposed 4 days in the greenhouse contained, at the end of that time, no oxygen determinable by absorption in alkaline pyrogallol according to the usual gas-analysis methods. That no substances deleterious to the plants were given off by the rubber of the gas bags is shown by the fact that even the plants most sensitive to disturbances of the soil atmosphere grew satisfactorily with

the gas bags attached, provided the composition of the gas inside was suitable. Also, some experiments in which the gas supplied was controlled in glass gasometers instead of in rubber gas bags showed essentially the same results as did the experiments with the bags.

The oxygen and nitrogen used in the experiments were commercial gases, purchased in compressed form in cylinders, from the Linde Air Products Company. These gases are made by the fractional distillation of liquid air and contain practically no impurity except that each gas may contain traces of the other. The traces of nitrogen present in the oxygen are unimportant. Traces of oxygen in the nitrogen are usually so small as to be negligible in ordinary experiments. Where extreme precision was required in the removal of all oxygen the nitrogen was thoroughly washed with alkaline pyrogallol before use. In a few cases, also, nitrogen was prepared from air by removing the oxygen with this same reagent. No attention was paid to the traces of argon and other rare gases doubtless present in all of the gases used.

The soil used in the experiments was of several types. For most cases a rather heavy loam of quite ordinary character was used alone or mixed with from one half to three times its volume of fine quartz sand. Each of three other loams was used for a few experiments, and in a few cases humus, stable manure, ground bone or ground feldspar was added to one or more

of the soil mixtures. Similar results were obtained with all soils used and it seemed useless, therefore, to examine or define the soils in detail. The admixture of more or less sand with the loam served, in connection with the mercury column of the auto-irrigator, to regulate the water content of the soil. The heavier (less sandy) mixtures were used for the more water-loving plants. It will be remembered that the capillary tension, and hence the water content held against the auto-irrogator, is greater the finer the particles of the soil.

EXPERIMENTS WITH COLEUS.

In most of the experiments here reported the plant used was Coleus blumei, this species being selected because of the ease with which it can be grown under glass at any season and also because its soft and fleshy stem of nearly square cross-section makes it particularly suitable for developing and testing a technique of sealing which may be expected to be widely applicable to other species. In various experiments four strains ~~as~~ or sub-varieties of Coleus were used, these differing in color, leaf form, and the like, as is characteristic of this species. Results with all four strains were essentially alike and have been repeatedly obtained in three successive seasons, from 1915 to 1917. The behavior of Coleus on the exclusion of oxygen from the roots, according to the method described in the last chapter , is typified by the following history of plant number 209.

History of Coleus blumei Plant No. 209.

May 8, 1916.	Potted; watered thereafter by hand.
July 11, 1916.	Connected with auto-irrigator and sealed; outlet tubes left open to atmosphere.
July 24, 1916.	Condition and growth rate of plant were normal.
July 25, 1916.	Replaced soil atmosphere with nitrogen.
July 28, 1916.	Plant showed slight wilting.
July 29, 1916.	Wilting was more severe and increased in severity thereafter.
Aug. 7, 1916.	On removing plant from pot the roots were found to be dead.

The intake of water by this plant during the period covered by the above history, is given in the table below. It is obvious that the actual intake of water by the plant will depend on the intensity of transpiration which depends, in turn, on the evaporating power of the air.[1] Because of this, and in order to obtain data which are comparable from day to day it is necessary to compute the water-intake relative to the loss of water from a porous cup atmometer[2] over the same period. This ratio is given in the last column of the table and corresponds to the similarly comparable transpiration ratio called by Livingston the "relative transpiration".

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[1] Livingston and Hawkins,- Car. Inst. of Wash., Pub. 204, pp. 5-48 (1915); Free,- Studies in Soil Physics, pp. 18-26 (1912).

[2] On the porous cup atmometer and its use see: Livingston,- Plant World 18: 21-30, 51-74, 95-111, 143-149 (1915).

Water records of *Coleus blumei* plant No. 209.

Time of Reading		Water taken from reservoir (cubic centimeters)	Atmometer Reading (cubic centimeters)	Ratio $\frac{\text{Water intake}}{\text{Atmometer Reading}}$
Date	Hour			
July 18, 1916	2:00 p.m.	(readings begun)		
" 19, "	5:00 p.m.	5	16.0	.313
" 20, "	6:00 p.m.	30	--	--
" 21, "	2:00 p.m.	25	24.7	2.227
" 22, "	5:30 p.m.	30	12.0	2.500
" 23, "	5:00 p.m.	35	10.2	3.431
" 24, "	5:00 p.m.	40	12.6	3.175
" 25, "	3:15 p.m.	15	4.5	3.333
" 26, "	3:15 p.m.	12	5.3	2.263
" 27, "	5:30 p.m.	23	13.7	1.679
" 28, "	1:00 p.m.	15	4.6	3.261
" 29, "	6:00 p.m.	0	18.5	0
" 30, "	5:00 p.m.	0	12.0	0
" 31, "	5:00 p.m.	0	11.7	0
Aug. 1, "	1:30 p.m.	0	14.3	0
" 2, "	3:15 p.m.	0	20.7	0
" 3, "	4:30 p.m.	0	13.8	0
" 5, "	1:00 p.m.	0	14.2	0
" 6, "	7:00 p.m.	0	13.4	0
" 7, "	1:00 p.m.	0.	6.8	0

It is apparent that there was a complete cessation of water-intake by the plant on July 28th, and, by referring to the history as cited above, it is seen that this is just 3 days after the soil atmosphere was replaced by nitrogen. This cessation of water-intake was accompanied, also, by slight visible wilting of the plant although severe wilting did not occur until several days later. The variations of water-intake prior to its complete cessation on July 28th may be due either to spontaneous variations in the transpiring power of the plant or to some failure of complete equivalence between the water-intake by the plant and the water-loss from the reservoir, caused, perhaps, by the occasional irregularities in the hour of reading the water-loss. Whatever be the cause of these variations they are unimportant since they are much less marked than the complete cessation of water-intake on July 28th.

These two symptoms, the cessation of water-intake and the appearance of visible wilting, are the invariable sequentia of replacing by nitrogen the oxygen-containing atmosphere about the roots of Coleus. If the removal of the oxygen is permanent the wilting and cessation of water-intake are followed in a few weeks by the death of the plant. However, if air or oxygen be forced through the soil after the symptoms of injury have occurred but before the plant is dead, the plant usually recovers, although the recovery is slow and not always complete. The

results of a number of experiments are given in summary in the following table.

Records of Coleus deprived of oxygen.

(Figures are numbers of days after first removal of oxygen)

Experiment number	Wilting visible	Water intake stopped	Oxygen Re-supplied to roots	Recovery ~~ing~~ perceptible	Recovery apparently complete
1	9	9			
2A	4	4	8	47	80
3	5	no record	12	28	42
4	5	"	10	20	60
6	9	8	10	16	47
16	2	1	2	32	
201	4	no record	6	12	20

Two of these plants, after recovery from the first application of nitrogen were again supplied with this gas in place of oxygen. These were plants number 3 and number 201. In both cases the same symptoms of injury recurred; in number 3 after 7 days, and in number 201 after 4 days. To one plant (not included in the above table) nitrogen was applied for only one day, being then replaced by air. There was no apparent injury and no cessation of water-intake. The plant continued to grow normally. To five plants oxygen was applied as in the usual gas bag technique. Neither injury nor benefit was perceptible. To two plants ordinary air was applied, but in closed gas bags according to the usual technique. One of these plants was uninjured after 50 days when the experiment was stopped. The other plant wilted after 12 days and ultimately died. To one plant the seal about the stem was applied as usual but the tin top to the can was omitted, leaving the soil exposed to the air. This plant grew normally and showed no injury. In two cases injury occurred after sealing but with the gas outlet tubes still open to the air, the times of appearance of wilting being, respectively, 13 and 17 days after sealing. In both cases the symptoms of injury were exactly as described above, the intake of water ceasing after 11 and 7 days, respectively.

The effect of decreasing the amount of oxygen in the soil atmosphere, without removing it entirely is indicated by the data of the following table. The gas supplied was changed daily.

Records of Coleus on diminished oxygen.

Experiment number	Oxygen in the soil atmosphere (Volume percent)	Time after which wilting was visible (days)	Time after which water-intake ceased (days)
202	10	7	no record
206	10	9	8
205	6	9	9
204	2	6	6

In summary of all results it may be said that Coleus is injured in from 2 to 10 days after the normal soil atmosphere is replaced by an atmosphere of nitrogen. When the concentration of oxygen in the soil air is diminished injury also occurs, possibly a little less quickly. Apparently the decrease of oxygen supply suffered when a plant is sealed-in but with the outlet tubes left open is also sufficient to cause injury, but in this case the appearance of the injury is clearly later than when the exclusion of oxygen is complete. The symptoms of injury are wilting and a cessation of water-intake by the plant. Usually the water-intake ceases a few hours or more (sometimes several days) before wilting of the leaves is perceptible.

On examining the roots of plants which had been injured by exclusion of oxygen the root-systems were found to be dead and decayed. When the injury was recent the visible decay of the roots was partial. Roots were determinately dead only in parts of their length, regions of brown discoloration alternating with regions of apparently healthy root. After long-continued exclusion of oxygen the entire root-system was invariably found to be dead. In all of the plants which were first injured and then revived by the re-admission of air or of oxygen, the original root-system was found to be dead. The recovered plant was supplied by a new root-system starting always from the lower end of the stem. In no

case were these new roots observed to start from any part of the original root system and in no case was any part of the original root-system found to be still alive. The new root-system formed on the re-admission of oxygen was found, in every case, to be composed of a few long and thin roots, very little branched. The normal root-system, on the other hand, is much branded and the individual roots are relatively much thicker and shorter. It is by no means certain, however, that this difference in the appearance of the old and new root systems has any relation to the oxygen supply. More uniform water conditions, the absence of light, or the lack of mechanical stimuli to the roots in plants the stems of which were rigidly supported by the seal, may be sufficient to account for these differences. In the two cases in which the oxygen was removed a second time (after recovery from the previous injury) the new root system was formed as before, but the roots of this new system were also injured and discolored precisely as in the cases of injury to ordinary roots.

In one case a mixture of 50 percent carbon dioxide and 50 percent oxygen (by volume) was applied to the roots. The plant was slightly wilted after 7 days and badly wilted after 11 days. However the water-intake did not cease as in the plants supplied only with nitrogen. On examining the root-system it was found to be dead throughout there being no visible evi-

dence of the alternation of dead and apparently healthy portions as observed in the other cases. This plant was supplied with ample oxygen and the injury probably may be ascribed to some specific effect of carbon dioxide. It would be unsafe, however, to base any important conclusions on a single case.

EXPERIMENTS WITH HELIOTROPE.

The experiments were made on seedling plants of the common florists' variety of *Heliotropium peruvianum* grown in a soil of one half loam and one half sand, by volume. The technique was the same in all particulars as that described for Coleus. The plants were practically mature when tested. Two plants were treated by replacing the normal soil atmosphere with nitrogen. In both cases the plant wilted, much as happened in the case of Coleus, the wilting beginning to be visible approximately 25 and 38 hours respectively, after the soil atmosphere was replaced. Re-supply of oxygen to the roots did not induce recovery. In both cases the wilting progressed rapidly and the plants died within a few days. The cessation of water-intake which accompanied the wilting of Coleus did not occur with Heliotrope until the plants were completely wilted and nearly all of the leaves were black and entirely dead. However, a slight decrease in the amount of water taken in occurred coincidently, or nearly so, with the beginning of wilting and the amount of water-intake decreased gradually thereafter until the final stoppage. Examination of the roots showed that the root systems were entirely dead and badly disintegrated, but this examination was not made until after the complete death of the aerial portions. No roots were examined soon after

injury. That the injuries observed were not due to the seal or to any accidental feature of the technique was shown by the normal behavior of a control plant grown coincidently and in the same manner but supplied with oxygen instead of nitrogen.

EXPERIMENTS WITH OLEANDER.

The plants were rooted cuttings of *Nerium oleander*, 15 centimeters high and grown in soil consisting of 2 parts loam and 1 part sand, by volume. The technique was the same as with Coleus. Two individual plants were tested with nitrogen in the usual manner, controls being provided as before. No injury was observed for 14 and 12 days, respectively. At the end of these times the leaves nearest to the base of the stem began to turn yellow and fall off. This yellowing extended in a few days to the leaves next above, and thus progressed slowly up the stem, but at a slow rate. The top leaves of both plants were apparently still healthy when the experiments were stopped, after 43 and 25 days respectively. At no time was there any determinable slowing of the water-intake nor was there any perceptible wilting. Normal oleander plants, when deprived of water, show a characteristic spiral curling or rolling-up of the leaves which apparently corresponds to wilting in such species as Coleus. This was not observed in the plants treated with nitrogen. After the experiment the root-systems of both oleanders were found to be dead and much decayed, the injury to the roots being much more severe than to the tops. No tests were made as to the possibility of recovery on the re-admission of oxygen.

EXPERIMENTS WITH WILLOW.

The experiments were made with rooted cuttings of a species of swamp willow growing wild near Baltimore and which is either *Salix nigra* or a closely related species. The technique was as usual, the soil being loam without sand. No injury of any kind was observed in two plants which were treated with nitrogen. Normal health and growth continued for 43 days and 29 days respectively. After the first nine days the first plant was supplied with boiled water and every possible precaution was taken to prevent the entry even of traces of oxygen. The second plant was treated similarly during the entire experiment. On the 33rd day the nitrogen was removed from the first plant and carbon dioxide was substituted, care being taken not to admit traces of oxygen. The plant remained on carbon dioxide until the 43d day, when the outlet tubes were opened to the air. This was on August 7, 1916. During the remainder of the summer the plant continued in this condition, the outlet tubes being open. Water continued to be supplied by the auto-irrigator. Late in October the plant lost its leaves and passed into the resting state. It was kept in the greenhouse during the winter and put out new leaves on April 8, 1917. It is now (April 28, 1917) again under test with nitrogen. At all times the behavior of this plant has been normal and exactly the same as that

of control plants grown at the same time. The behavior of the second plant was also normal during the period of experiment with it. The water-intake of both plants was comparable in all ways with that of the controls. Further experiments are in progress with this species, but present evidence seems sufficient to show that the roots remained uninjured by a removal of oxygen which must have been very nearly complete if not quite so.

EXPERIMENTS WITH EUCALYPTUS.

One individual was employed, being a seedling of Eucalyptus robustus about 30 centimeters high at the beginning of the experiment. The technique was as usual, the soil being one-fourth loam and three-fourths sand. During 55 days since the replacement of the soil atmosphere by nitrogen the health growth and water-intake of the plant have continued apparently normal and the plant is still (April 28, 1917) in excellent condition. No control plant has been grown.

EXPERIMENTS WITH OPUNTIA.

The plants were young natural seedlings of Opuntia versicolor collected at Tucson, Arizona, by Dr. W. A. Cannon. When received in the laboratory the stems were 6 to 10 centimeters long and were in resting condition. They were planted in a soil consisting of two parts sand and one part loam and irrigated with the auto-irrigator, as usual. In the week beginning March 18, 1917, new growth began in three of the plants and on March 22, 1917 one of these was sealed and supplied with nitrogen according to the usual technique. Nothing corresponding to wilting could be detected in small plants of this character and the water-intakes of all of the plants were so small in total quantity that variations were undeterminable. However the new leaves of the plant supplied with nitrogen stopped growing immediately and became darker in color, while the growth-rate and color of the new growth on two of the control plants remained normal. After 23 days on nitrogen the roots were examined. All small roots were found to be dead and badly decayed and the lower half of the fleshy main root was also decayed.

PHYSIOLOGICAL CONCLUSIONS.

There can be almost no doubt that the injuries observed with Coleus and Heliotropium were actually caused by deficient oxygen in the soil. The harmlessness of the technique of sealing and the suitability of the experimental conditions for the growth of the plants are attested by the satisfactory growth of many controls and by the recovery of several injured plants after the admission of oxygen. Any theoretical possibility of error due to a specific poisonous action of the kind of nitrogen used or of any impurity in it is removed by the agreement between the effects of commercial nitrogen and of nitrogen prepared from air. Any other form of accidental injury is excluded by the complete agreement of the several independent tests.

It is conceivable that the injury caused by the removal of oxygen may be either a direct response of the roots themselves to oxygen deficiency or an indirect effect through some change produced in the soil. The exclusion of oxygen from the soil probably has important effects on the quantity and character of the soil micro-organisms and it is possible that such alterations of the micro-flora may react upon the plant roots. However, any modification of the soil micro-flora or any similar changes which might be responsible for secondary effects on the roots would be expected to be different in different soils. The original floras of any two soils

are usually unlike and probably would not respond in an entirely identical manner to the removal of oxygen. In the experiments with Coleus three quite different loams from different localities were used and were mixed with varying proportions of sand. Some of the soils were high in organic matter, some were low. Some were light in texture, some were fairly heavy. With all of these varied soils the results were completely identical, both in the conditions determining the occurrence of injury and in the symptoms of the injury which occurred. This absence of any dependence of the results on the nature of the soil implies that such modifications of the soil micro-flora as occur under the conditions of these experiments are without important influence on the roots. It is highly probable that the injuries observed are due to changes in the roots themselves which changes result directly from the shortage of oxygen.

The obvious hypothesis as to the mechanism of these injuries is that they are due to direct interferences with the respiration of the root protoplasm. It is probable that any tissue which requires free oxygen for respiration can absorb this oxygen from any atmosphere in which oxygen is present in sufficient total quantity, regardless of the percentage or partial

pressure of the oxygen.[1] Thus oxygen will be obtained quite as well from an atmosphere of low oxygen content as from one of high if both atmospheres are sufficient in total volume or are renewed sufficiently often. If this is true and if the observed root injury is due to interference with respiration, the roots should be able to endure a low percentage of oxygen in the soil atmosphere if the atmosphere is renewed sufficiently often. The agreement of the Coleus results with this prediction is not as complete as might be desired. Atmospheres containing 2, 6 and 10 percent of oxygen were found to be injurious, though they were changed daily. Even the simple enclosing of the soil, the outlet tubes remaining open, was injurious in some cases. Sealed plants grew in completely normal manner only when supplied with pure oxygen or when air was actually

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[1] See authors cited in note , page , also: Godlewski,- Jahrb. wiss. Bot. 13: 491-522 (1882); Stich,- Flora 74: 1- (1896); Pfeffer,- Physiology of Plants, vol. 1, p. 539 (1900); Czapek,- Biochem. der Pflanzen, vol. 2, p. 394 (1905); E~~y~~uler,- Pflanzenchem. vol. 2 & 3, p. 166 (1909); Bayliss,- Prin. General Physiol. pp. 608-609 (1915).

drawn through the soil.

It is probable that this occurrence of injury with the soil atmospheres of lower oxygen content, even when these were changed frequently, is due to insufficient diffusion of the oxygen in the soil itself. The place where oxygen must be supplied is at the roots, not merely within the pot. It is probable that the internal distribution of the oxygen through the soil is regulated by the same diffusional principles which have been described as controlling the exchange of oxygen between field soils and the general atmosphere. In the experiments with atmospheres of low oxygen content the oxygen may have disappeared altogether in parts of the soil although still available in other parts or in the sealed space above the soil. For satisfactory determination of these questions it would be necessary to experiment with moving atmospheres or with special devices for maintaining a substantially uniform gas composition in all parts of the soil.

The hypothesis that injury is due merely to interference with the respiration of the root protoplasm is supported by a general impression derived from the experimental results to the effect that injury is likely to be manifested a little more quickly with plants of large root systems than with plants the roots of which are few. The available data do not have sufficient quantitative accuracy to permit actual test of

this suggestion. All that can be said is that the plants which appeared to have the larger root systems were in several cases injured more quickly. In all cases the time required for injury to become manifest is subject to much variation, as is indicated by the detailed data given on page 17[illegible]. Probably these variations are due to incomplete removal of the original soil atmosphere at the beginning of an experiment. The removal of this original atmosphere must be accomplished by sweeping it out with the nitrogen (or other gas) which is to replace it. This replacement cannot be expected to be entirely complete unless an impossibly large amount of nitrogen is run through. Accordingly a certain amount of oxygen will be left behind and must be used up by respiration before injury will occur. The actual time of appearance of injury will depend upon (1) the amount of oxygen left in the pot at the beginning of the experiment, (2) the rate at which this oxygen is used up, and (3) the degree to which the oxygen content in different parts of the pot is equalized by diffusion or in some other way.

Whether or not the injury to Coleus be regarded as due to a disturbance of root respiration, it is interesting that the local injury manifests itself in the economy of the plant as an interference with water-absorption by the roots. This follows both from the main symptoms of injury, namely wilting ~~and stoppage of water intake~~ and from the observed

cessation of water-intake. Indeed, in most cases this cessation of water-intake precedes slightly the appearance of visible wilting in the leaves. If the injury progresses slowly, as when the outlet tubes are open and the air supply is merely restricted, the cessation of water-intake may precede the visible wilting by several days.[1] With heliotrope and oleander the effect on water-absorption does not appear to be the same as in Coleus, since the water-intake of the heliotrope decreases only slowly and that of the oleander not at all. Evidently these three species differ in the degree to which the absorption of water by their roots depends upon the life or health of the root protoplasm. Watson[2] has observed the absorption of water by roots which are entirely dead, and it will be recalled that the experiments of Kosaroff described above indicated this same possibility though the absorption was less than through living roots. Kosaroff's experiments led, also, to the same conclusion reached in the present work, namely, that one effect of lack of oxygen in the soil is to decrease the water absorbing power of the roots.

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[1] See pages

[2] Ann. Bot. 8: 119-120 (1894).

The ability of the roots of willow and eucalyptus to survive long periods of oxygen deprivation without apparent injury to the plants suggests that these roots may be capable of respiring entirely anaerobically. The data imply that this is true, but the affirmative answer can not be given with entire assurance. It is possible, that some small source of oxygen was neglected accidentally or escaped the precautionary expedients of the experiments. It is possible, also, that the traces of oxygen which doubtless remained in the pots at the beginning of the experiments may have sufficed for a measure of root respiration over the whole period of inclosure. Certainty as to the possible anaerobic life of these or other roots can be reached only by the repetition of the experiments often enough to exclude the possibility of accidental error. In any event there can be no question that Coleus, and heliotrope differ markedly from willow and eucalyptus in the amount of oxygen needed by the roots, and that the last named plants require at most only an extremely small amount. On the face of the experiments they require none at all.

The single experiment on the effect of carbon dioxide on Coleus indicated some specific poisonous action of this gas, but this is obviously not general since there was no effect on willow with a much longer exposure. It is interesting that the application of carbon dioxide to Coleus did not stop the water-intake though it did cause wilting and death.

ECOLOGICAL CONCLUSIONS.

The ecological significance of the results here reported lies in the wide differences found to exist between different species in the oxygen requirement of their roots. Coleus and heliotrope are injured by a very slight deficiency of oxygen. Oleander is injured after a time but is much less sensitive. Willow and eucalyptus can live with very little soil oxygen, possible with none. A similarly wide difference exists in the behavior of the roots of Coleus and willow toward carbon dioxide. The experiments of Cannon already described show similar differences between *Opuntia versicolor* and *Prosopis velutina*, the Opuntia being more sensitive to low oxygen and high carbon dioxide than is the Prosopis. This conclusion of the sensitiveness of Opuntia is confirmed by the single test of this species which is included in the present experiments.

The ecological bearing of these facts is obvious and has been discussed already by Cannon and Free.[1] If differences as wide as this exist in the response of different species to the composition of the soil air it is manifest that soil aeration may be a much more important ecological factor than is generally assumed,

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[1] Science *45*: 178-180 (1917).

perhaps quite as important as water-supply or temperature. It will be necessary to distinguish between habitats on the basis of the good or bad aeration of the soil and between species on the basis of their varying susceptibility to these conditions.

For the species investigated so far there is good correspondence between the sensitiveness to aeration and the ecological habit. Coleus and heliotrope, which are very sensitive are known to prefer open and well-drained soils in which aeration is presumably good. On the other hand the willow, which is not sensitive, is a swamp plant capable of growing where aeration is certainly very poor. The same is true of the eucalyptus though this plant has a much wider distribution than the willow, being capable of growth on well-drained soils as well as in poorly drained ones. Probably this difference is due to the relations of the two species to water. The willow is insensitive to aeration but very sensitive to water-supply, being most at home only in the wetter soils. The eucalyptus is comparatively insensitive to water-supply as well as to aeration. The oleander, which is intermediate in sensitiveness to aeration is also intermediate in distribution, preferring neither the extreme openess suitable to Coleus and heliotrope nor the extreme wetness endured by the willow and eucalyptus. The desert plants Opuntia and Prosopis show a similar correspondence between oxygen requirement and distribution.

The Opuntia which is sensitive to aeration, grows only on the well-drained slopes and hill sides. The Prosopis, which is less sensitive, prefers the stream banks and valley-flats where water is more plentiful and aeration less good.

The detailed application of these concepts to problems of plant distribution is impossible in the present ignorance of the responses of most species to aeration differences. The methods of the present investigation, or some equivalent methods, must be applied in detail to a wider range of species just as actual tests of temperature and moisture responses have been applied already. However, the present data justify the conclusion that these aeration responses cannot be neglected and suggest that they may furnish the key to some of the facts of plant distribution which are anomalous on the present theoretical basis.

AGRICULTURAL CONCLUSIONS.

The meaning of these results for agricultural practice is essentially the same as their meaning for ecology. If species vary in response to soil aeration it is obvious that the cultural importance of this factor will depend upon the particular crop concerned. Doubtless certain crops will require very perfect soil aeration. Probably others will grow successfully with poor aeration or even with none. As before, detailed applications to practice and theory must await specific knowledge of the aeration responses of the individual crop plants. The relations of crops to temperature and moisture have long been recognized as important and have received consideration in practice. To these factors there must now be added the third one of soil aeration and it must be realized that the variations of crops in this regard are as important and probably as wide as they are in regard to temperature and moisture. The present practice of assuming that a maximum of soil aeration is desirable or necessary for all crops is as unsound theoretically and probably as foolish practically as it would be to assume that all crop plants required a maximum of water or the highest possible temperature. Just as each crop has an optimum of water supply and an optimum temperature so it has probably an optimum degree of soil aeration. To take account of this in the formulation of an

agricultural regimen may mean not only a possible saving by avoidance of excessive and unnecessary procedures to encourage aeration but also an actual improvement of production through better adjustment of conditions to the specific needs of each individual crop.

SUMMARY OF CONCLUSIONS.

The one conclusion from these experiments which may be regarded as satisfactorily certain is that different species of plants differ in the oxygen supply necessary for their roots. It follows that there are differences in the response of different species to different degrees of soil aeration and that these differences are probably important ecologically and agriculturally.

It is a reasonable inference from the data but is not fully certain that the injuries worked in certain plants by deficiency of oxygen in the soil are due to interferences with the respiration of the root protoplasm. In Coleus this seems to affect first the water-absorbing power of the roots. This is probably not true of the other species tested.

The two experiments with carbon dioxide indicate that this gas has a specific poisonous effect on Coleus but none on willow.

VITA.

The writer was born at Dagus Mines, Pennsylvania, May 3, 1883. In 1906 he received the degree of Bachelor of Arts from Cornell University. From August 1906 to September 1907 he was assistant chemist in the Agricultural Experiment Station, Tucson, Arizona. From 1907 to 1912 he was scientist in the Bureau of Soils, United States Department of Agriculture. From 1912 to 1914 he was in private practice as a chemical engineer in San Francisco, California. Since October 1914 he has been a student in the Department of Plant Physiology of the Johns Hopkins University.

Figure 1

General arrangement of culture can.

Figure 2

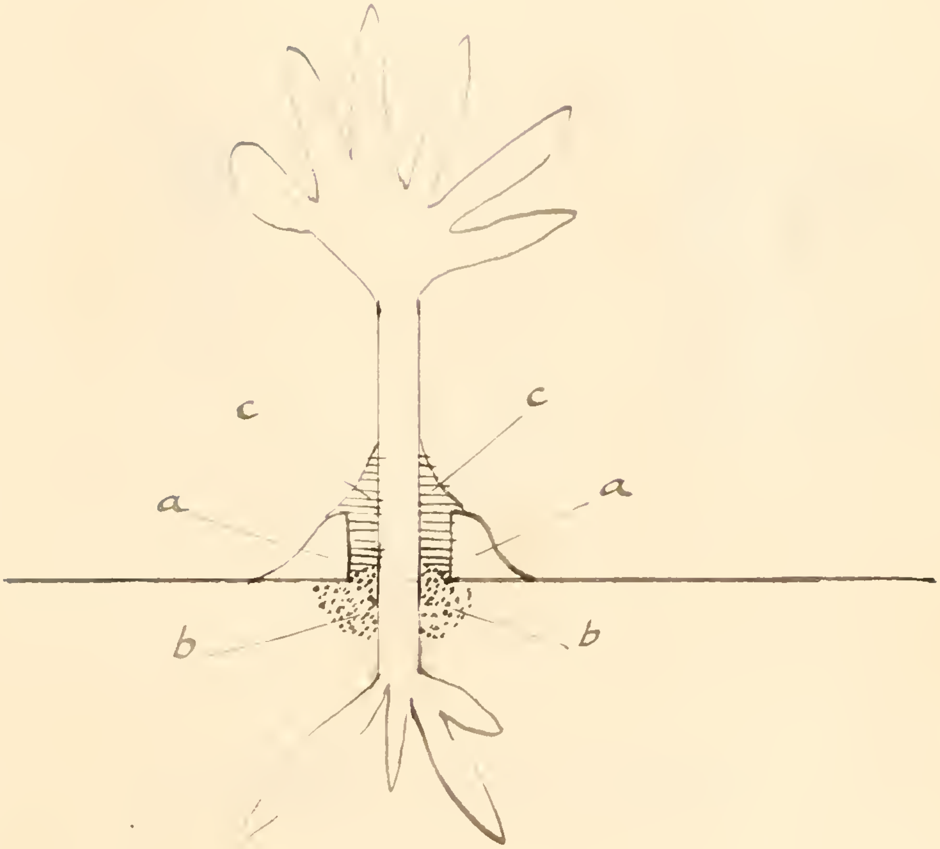
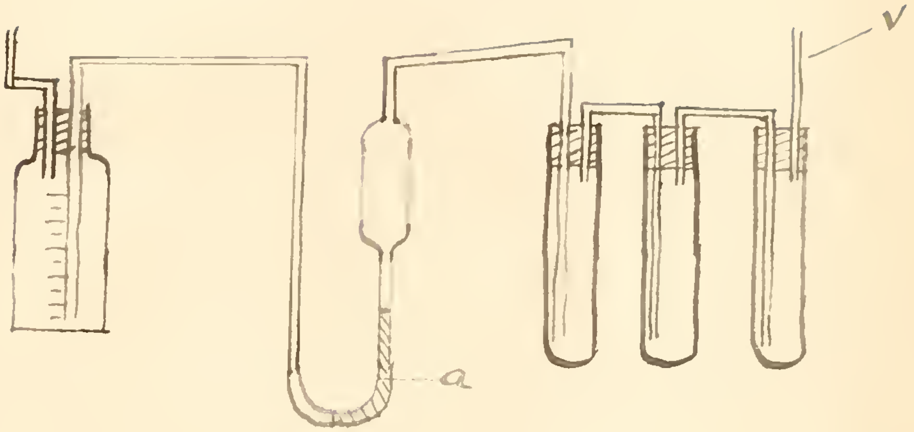


Diagram of Seal.

Figure 3



Arrangement of irrigator system

Figure 4

Arrangement of apparatus for several cultures.

Figure 5.

Arrangement of gas bags.